GUIDELINES FOR COCCOLITH AND CALCAREOUS NANNOFOSSIL TERMINOLOGY

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ABSTRACT. The descriptive terminology applicable to coccoliths and other calcareous nannofosils is reviewed and revised. A listing of about 400 terms is given with brief explanations and explanatory figures. General terms are given first, followed by terms for specific taxonomic groups. Appendices list terms we have not used and summarize terms, such as caneolith, which have been proposed for particular types of coccoliths.

THE descriptive terminology of coccoliths evolved on an *ad hoc* basis until the 1950s. Then, the development of electron microscopy stimulated a major revision and introduction of new terms in a co-operative effort (Braarud *et al.* 1955*a*, 1955*b*; Halldal and Markali 1955; Hay *et al.* 1966). This concentrated on the standardization of names for the distinctive types of coccoliths found on coccospheres, e.g. placolith, caneolith. Subsequent work on diverse fossil coccoliths led to a different approach concentrating on element-level structure. The appropriate terminology was synthesized during a Round Table Session at the Rome 1970 Plankton Conference (Farinacci 1971).

There has been intensive research on coccoliths since 1970 and so the existing guides have become obsolescent. In response to this, a terminology workshop was held during the International Nannoplankton Association (INA) conference in Prague, 1991. Following this, a working group was set up and a two-day workshop held in London in 1992. Various publications have resulted from these discussions. Young (1992*a*) discussed new recommendations on controversial topics. Burnett and Bown (1992) provided a check-list for systematic descriptions. Van Niel (1994) reviewed in depth the descriptive terminology of nannoconids. Jordan *et al.* (1995) provided a glossary for living Haptophyta, including cytological terms and an overview of taxonomic concepts. The present paper represents the main proceedings of the working group, and is a synthesis of the descriptive terminology applied to coccoliths and other nannoliths based on its discussions.

In addition to the workshop discussions, this paper is based on a wide range of published sources including Braarud *et al.* (1955*a*, 1955*b*), Halldal and Markali (1955), Farinacci *et al.* (1971), Black (1972), Hay (1977), Okada and McIntyre (1977), Romein (1979), Aubry (1984, 1988*a*, 1988*b*, 1989, 1990), Theodoridis (1984), Perch-Nielsen (1985*a*, 1985*b*), Bown (1987), van Heck and Prins (1987), Varol (1989, 1992), Young (1989), Kleijne (1991, 1992, 1993), Young and Bown (1991), Young and Westbroek (1991), van Niel (1992), Heimdal (1993), and Winter and Siesser (1994). General works consulted include Brown (1954), Gower (1954), Fowler (1965) and Stearn (1983).

ORGANIZATION

The main text is organized into thematic categories covering different aspects of coccolith morphology. This is followed by a section on special terms needed for particular taxonomic groups. The paper is confined to the calcareous structures and does not consider organic components;

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terminology for these is reviewed in Jordan *et al.* (1995). Synonyms which we have not included in the main text are discussed in Appendix 1.

The terms recommended are italicized in the main text and given short explanations, the primary purpose of which is to explain the use of the term to coccolith workers, not to give a rigorous dictionary definition, still less an encyclopaedic explanation. The figures are meant to clarify the logic, but for various reasons not all terms are illustrated. For many terms, genera or species that show the feature particularly well are cited; good sources for illustrations of these taxa are Perch-Nielsen (1985*a*, 1985*b*) and Winter and Siesser (1994).

For terms which have been coined specifically for coccoliths (e.g. placolith) the original author is given in curly brackets {}; this information is mostly from Hay *et al.* (1966).

CHOICE OF TERMS

The general objective of the work is to summarize existing terminology rather than to create a new system. Nonetheless, in order to enhance precision it has been necessary in several cases to select between synonyms, or to assess the utility of obscure terms and, in a few cases, to coin new terms. The following principles have been used as guides.

Need. The purpose of specialist terminology is to make life easier for the reader, not for the author. The convenience of any terminological innovation should be weighed against the danger of producing unintelligible jargon.

Priority. Accepted usage must be respected. First usage and/or original definition is particularly important, but not necessarily binding.

Etymology. Words should not be given meanings that conflict with their etymology.

Ambiguity. Common words should not be given meanings that conflict with their normal meaning, or with their general scientific meaning, or that are more restrictive than a non-expert might reasonably anticipate (e.g. use of bar for structures with a particular optical orientation).

Obscurity. Obscure technical terms that are hard to remember and the meaning of which it is virtually impossible to guess (e.g. areolith), should be avoided, unless they are liable to be used so often that they will become part of routine vocabulary (e.g. placolith).

Synonyms and homonyms. As far as possible, only one term should be used for any given concept (poetic variation is not recommended). Equally, any given term should only have one meaning in a given context.

Where we have selected from possible alternatives, the others are discussed in Appendix 1 with a reference to it in the text – e.g. 'alternative spelling nanoplankton, see Appendix 1'.

GENERAL TERMS

Nannoplankton {Lohmann 1909} – plankton 2–63 μm in diameter (alternative spelling nanoplankton, see Appendix 1). Informal grouping including coccolithophorids, *Thoracosphaera*, chrysophytes, etc., but excluding the bacterial picoplankton.

Calcareous nannoplankton – nannoplankton with calcareous tests.

Nannofossil {?*Stradner* 1961} – fossil < 63 μm in diameter, excluding fragments and juveniles of larger fossils.

Calcareous nannofossil – nannofossil formed of calcium carbonate.

Coccolithophorid {Lohmann 1902} – calcareous nannoplankton belonging to the division Haptophyta (alternative term coccolithophore; see Appendix 1).

Coccosphere {Wallich 1860} – test of coccolithophorid (not necessarily spherical).

Coccolith {Huxley 1868} – calcareous structure formed by coccolithophorid.

Haptophyte – unicellular alga belonging to the division Haptophyta, includes all coccolithophorids (alternative term prymnesiophyte; see Appendix 1).

Nannolith {?Perch-Nielsen 1985*a*} – calcareous nannofossil lacking the typical features of calcareous dinophytes, heterococcoliths or holococcoliths and so of uncertain affinity (see also Young 1992*a*; Young *et al.* 1994). The division between coccoliths and nannoliths varies between authors and is liable to revision as new data become available. N.B. This rather restricted definition of the term has little etymological justification, but has been widely used, e.g. Perch-Nielsen (1985*a*, 1985*b*), Bown (1987), Aubry (1989). (The terms heliolith and ortholith provide an alternative basis for sub-dividing the calcareous nannofossils; see Appendix 1).

Heterococcolith {Braarud *et al.* 1955*a*, 1955*b*} – coccolith formed of crystal-units of variable shape and size. Crystal units typically arranged in cycles with radial symmetry.

Heterococcolithophorid – cell with coccosphere of heterococcoliths.

Holococcolith {Braarud *et al.* 1955*a*, 1955*b*} – coccolith formed of numerous minute ($< 0{\cdot}1\ \mu m$) crystallites all of similar shape and size (N.B. Many of the terms below are not applicable to holococcoliths, and there is a separate section for specific holococcolith terms).

Holococcolithophorid – cell with coccosphere of holococcoliths.

Combination cell {Thomsen *et al.* 1991} – cell with both hetero- and holococcoliths. N.B. These are thought to represent a transitional state between heterococcolithophorid and holococcolithophorid phases of the life cycle.

COCCOSPHERE RELATED TERMS

1. Descriptive terms

These are based largely on Okada and McIntyre (1977).

Monomorphic – all coccoliths of similar type (e.g. *Coccolithus*).

Dimorphic – coccoliths of two discrete types (e.g. *Scyphosphaera*).

Polymorphic – coccoliths of more than two discrete types (e.g. *Syracosphaera pulchra*).

Varimorphic {new} – coccosphere with coccoliths whose size and/or morphology varies according to position on the coccosphere (e.g. *Helicosphaera*).

Dithecate – with two discrete layers of coccoliths of different types (e.g. *Syracosphaera pulchra*).

Endotheca – inner layer of coccoliths of dithecate coccosphere.

Exotheca – outer layer of coccoliths of dithecate coccosphere.

Monothecate – with a single layer of coccoliths (e.g. *Scyphosphaera*).

Multilayered – with two or more layers of coccoliths but no differentiation into endo- and exotheca (e.g. *Emiliania*, *Florisphaera*, *Coccolithus pelagicus phase hyalinus*).

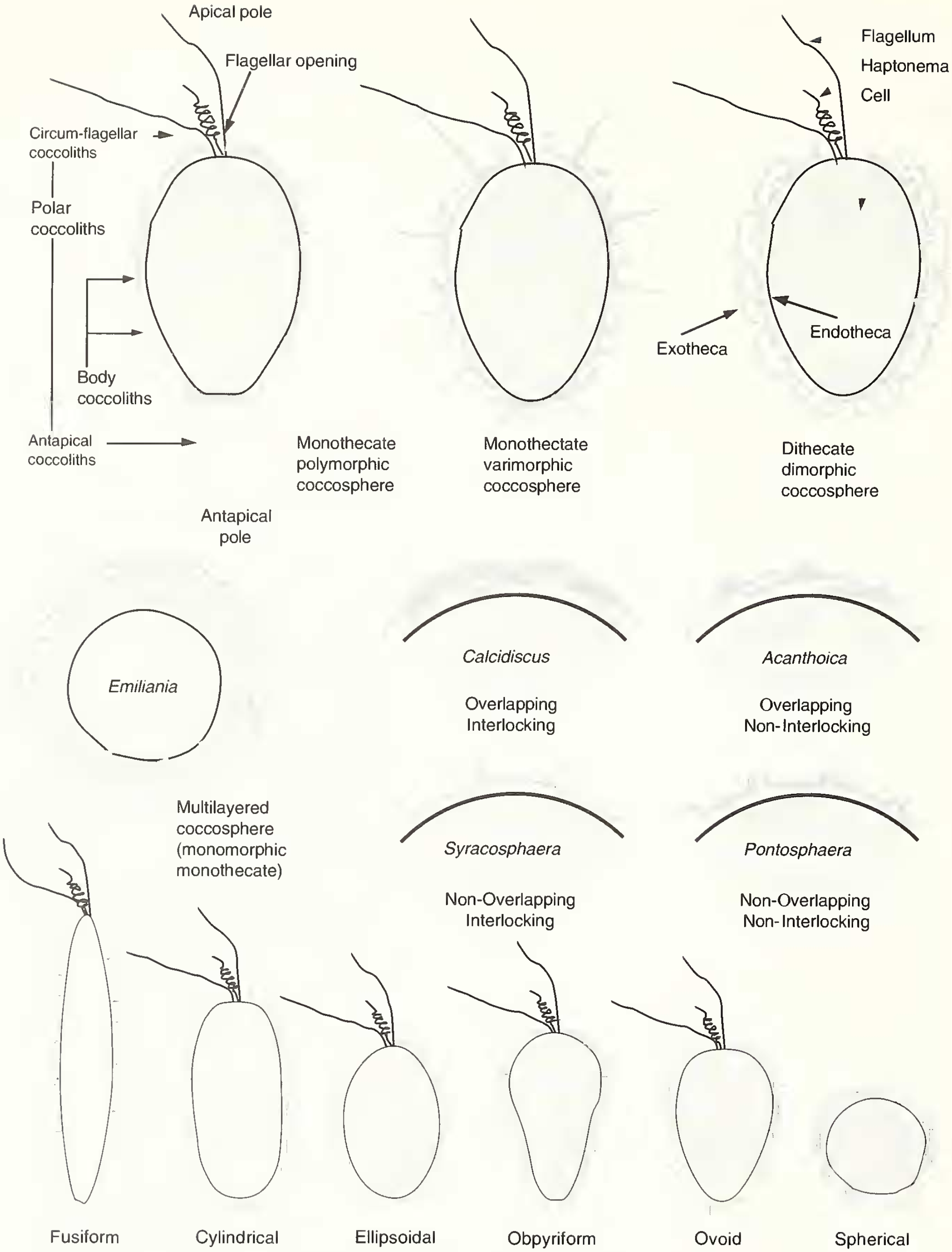
Xenosphere {new, from Greek *xenos*, stranger} – anomalous coccosphere containing coccoliths normally regarded as forming on quite discrete species (e.g. *Emiliania huxleyi* and *Gephyrocapsa oceanica*; Winter *et al.* 1979). N.B. These are very probably artefacts, the term is suggested specifically to suggest the abnormal nature of these structures.

Shape – coccospheres are three-dimensional so their shape should be described using appropriate terms for solid objects. Useful terms include: *cylindrical*, *ellipsoidal*, *fusiform* (elongate with tapering ends), *obpyriform* (inverse pear-shaped), *ovoid* (egg-shaped, i.e. one end broader than the other), *spherical*. See also Heimdal (1993) and Jordan *et al.* (1995).

2. Orientation

Apical pole – end of coccosphere with flagellar opening.

Antapical pole – opposite end of coccosphere.



TEXT-FIG. 1. Coccosphere related terms.

Antapical coccoliths – coccoliths occurring at antapical pole.

Body coccoliths – coccoliths other than polar coccoliths.

Circum-flagellar coccoliths/apical coccoliths – coccoliths occurring around flagellar opening (alternative term stomatal coccoliths; see Appendix 1).

Flagellar opening – opening in coccosphere through which the flagella and haptonema pass.

Polar coccoliths {Kamptner 1937} – coccoliths occurring at poles of coccospheres.

3. Coccolith arrangement

Overlapping – adjacent coccoliths overlap.

Non-overlapping – adjacent coccoliths arranged with edges directly abutting rather than overlapping.

Interlocking – adjacent coccoliths interlock.

Non-interlocking – adjacent coccoliths do not interlock.

N.B. Interlock and overlap are separate phenomena, and can occur in any combination (see Text-fig. 1).

4. Informal taxon-based terms

As with coccoliths (see below), various terms have been coined to refer to coccospheres of particular taxonomic groups. These do not need any special definition, beyond noting the taxonomic groups included. Examples are as follows.

Braarudosphere – Braarudosphaeraceae

Helicosphere – Helicosphaeraceae

TERMS FOR ENTIRE COCCOLITHS

1. Orientation

Proximal – directed toward centre of coccosphere/cell. On nannofossils this is usually assumed to be the concave side, but cannot always be determined.

Distal – directed toward outer surface of coccosphere/cell.

Horizontal – perpendicular to proximo-distal direction.

Vertical – proximo-distal direction.

Internal/inner/inward – toward centre of coccolith.

External/outer/outward – away from centre of coccolith.

Longitudinal – direction parallel to long axis of an elliptical/elongated coccolith.

Transverse – direction parallel to short axis of an elliptical/elongated coccolith.

End – edge of coccolith parallel to short axis.

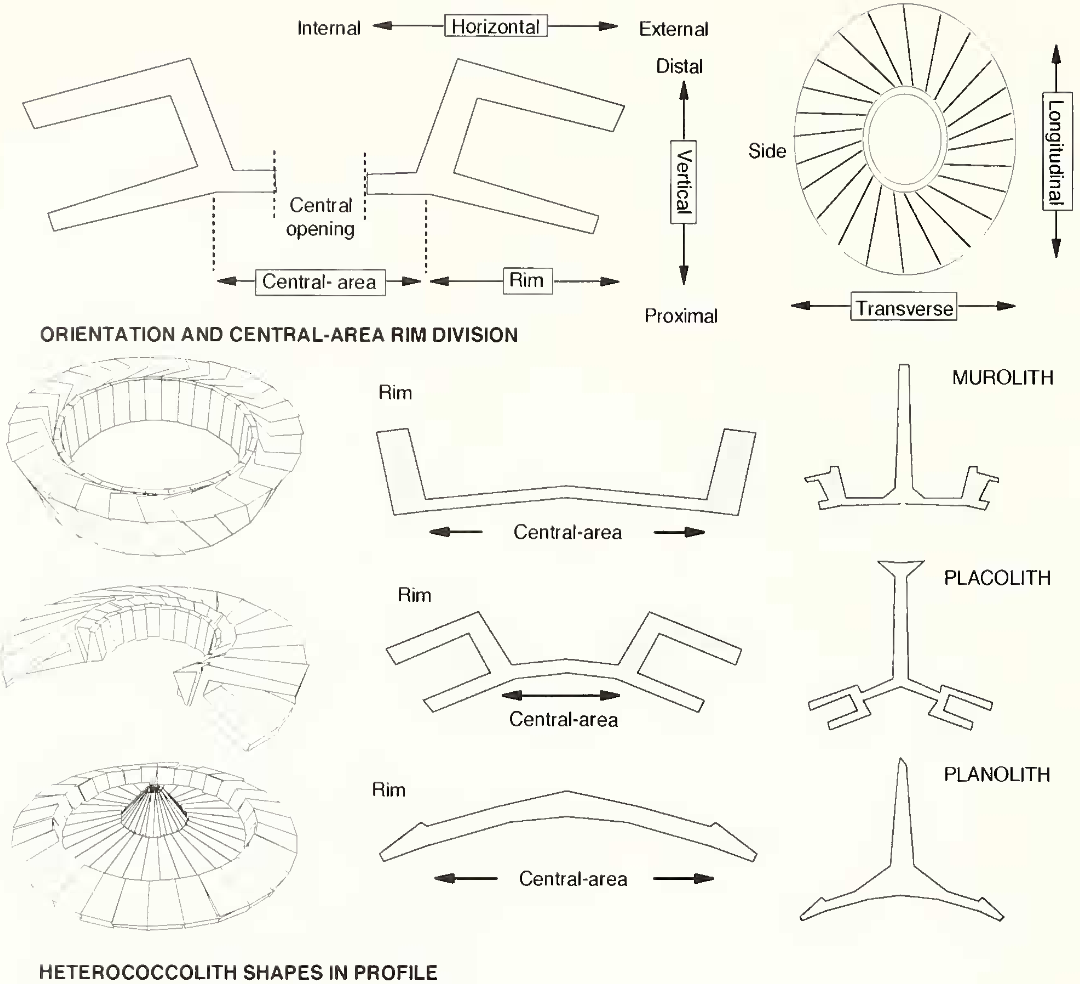
Side – edge of coccolith parallel to long axis.

Length/width/height – maximum dimensions of coccoliths in the longitudinal, transverse and vertical directions respectively.

2. Parts

In the vast majority of heterococcoliths there is an outer part which is somewhat higher than the inner part of the coccolith. This provides a convenient basis for starting any description of the shape and structure of coccoliths. It also is in large part a reflection of the coccolithogenesis process; growth outward and upward from the proto-coccolith ring forms the rim whilst growth inward forms the central area.

Central-area – inner part of coccolith, enclosed by the rim. Usually characterized by less regularly cyclical elements than the rim and by inward element growth. May be entirely closed, or include a central opening. N.B. We recommend hyphenating central-area since it has a special meaning.



TEXT-FIG. 2. Coccolith orientation, basic parts and shape in profile.

Rim – outer part of coccolith, usually characterized by regular cycles, some vertically directed structures and outward element growth (alternative term marginal area; see Appendix 1). N.B. Use of this term was agreed after considerable discussion at the workshops.

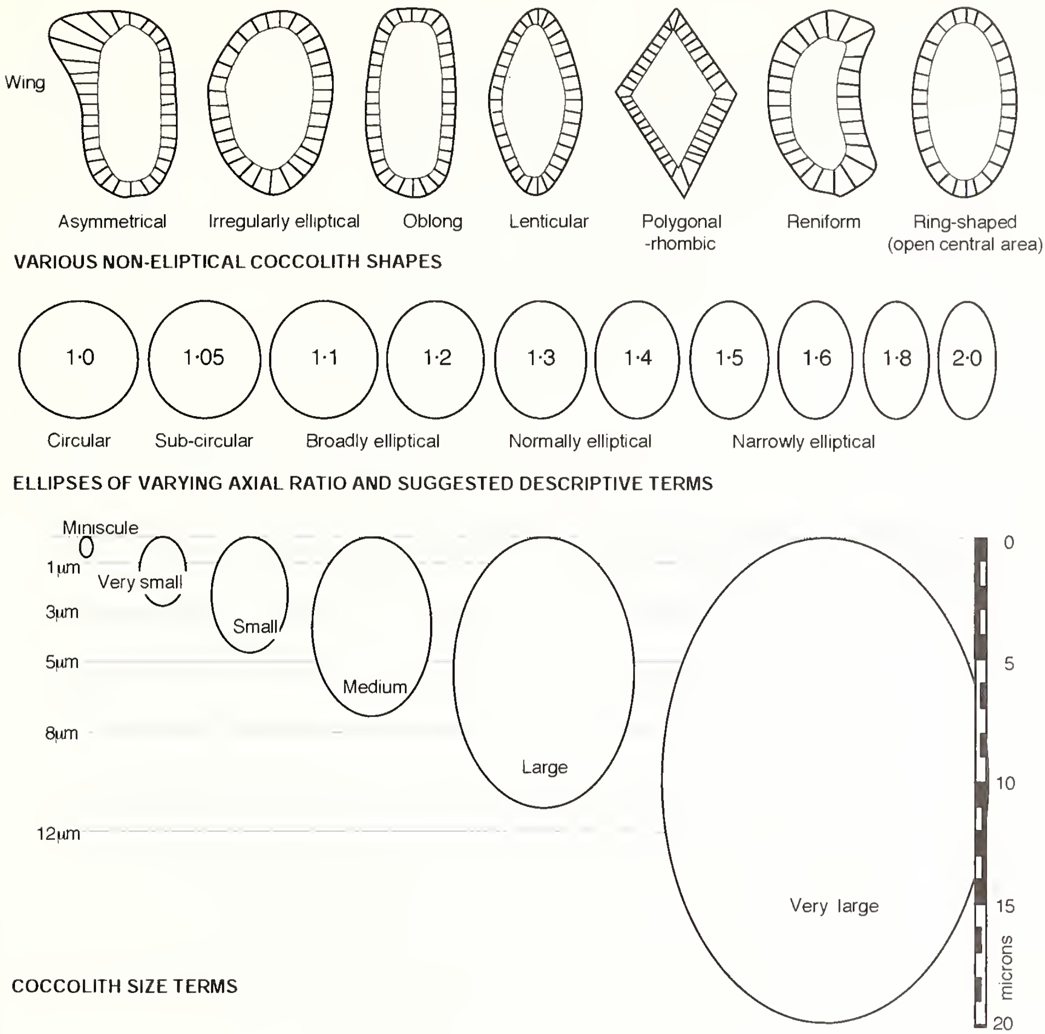
3. *Profile – coccolith shape in vertical cross section*

Although there is a very wide range of coccolith shapes, the three types listed below recur frequently in disparate groups (see also Young 1992*a*). They are probably homoeomorphic adaptations for organizing coccoliths on the cell. Intermediates between the types occur, and any of them can occur with or without processes. These terms have no taxonomic implications.

Planolith {Young 1992*a*, from latin *planus* flat} – rim not elevated (e.g. *Rhabdosphaera*, *Discoaster*).

Murolith {Young 1992*a*, from latin *murus* wall} – rim elevated but without well-developed shields (e.g. *Zeugrhabdotus*, *Pontosphaera*). (Discolith has been used in this sense; see Appendix 1).

Placolith {Lohmann 1902} – rim has two, or more, well developed shields (e.g. *Coccolithus*).



TEXT-FIG. 3. Coccolith sizes and shapes.

4. Outline – coccolith shape in plan view

Axial Ratio (abb. AR): ratio of length to width. Suggested descriptive terms, for elliptical coccoliths, are: *circular*; *sub-circular*; *broadly elliptical*; *normally elliptical*; *strongly elliptical.*

Asymmetrical – without bilateral symmetry, due to a wing or similar structure.

Elliptical – continuously curved with two axes of symmetry. Close to, but not necessarily an exact, mathematical ellipse (alternative terms *oval*, *ovoid*; see Appendix 1).

Irregularly elliptical – with an approximately elliptical shape but departing noticeably from regular form.

Lenticular – symmetrical form intermediate between a rhombus and ellipse, i.e. with pointed ends (e.g. *Syracosphaera prolongata*, *Stradnerlithus*).

Oblong – symmetrical form intermediate between a rectangle and ellipse, i.e. with curved ends but sub-parallel sides (e.g. *Calciopappus caudatus*, *Ellipsolithus macellus*). N.B. This is recommended botanical use (Stearn 1983).

Polygonal – with straight sides (triangular, pentagonal etc., e.g. scapholiths, *Corollithion*) (alternative term *geometric*; see Appendix 1).

Reniform – concavo-convex, kidney-shaped (e.g. *Nephrolithus*).

Ring-shaped – circular or elliptical, with narrow rim and open central area (e.g. *Cricosphaera*, *Manivitella*).

Wing – local extension of rim (e.g. *Helicosphaera*, *Kamptnerius*).

5. *Coccolith size*

Coccolith size is normally given as maximum dimension in plan view, i.e. length. The following sequence of terms is suggestions, based primarily on appearance under the light microscope.

Minuscule (< 1 μm), *very small*, 1–3 μm; *small* 3–5 μm; *medium* 5–8 μm; *large* 8–12 μm; *very large* > 12 μm.

6. *Informal taxon-based terms for entire coccoliths*

Many terms, defined originally as descriptive morphological terms, have become restricted taxonomically. For instance most authors would agree that the term helicolith should be restricted to coccoliths of Helicosphaeraceae, and not to any unrelated homoeomorphs. These terms are useful in many contexts, for example where it is important to distinguish between the organism and the coccolith/nannolith, or for describing polymorphic coccospheres. In general these terms are more widely used by workers on living coccolithophores than by palaeontologists. Comprehensive reviews are given by Tappan (1980), Chretiennot-Dinet (1990), Heimdal (1993), Siesser and Winter (1994) and Jordan *et al.* (1995).

We do not give detailed definitions here, since, essentially, they are defined by the characteristic morphology of the taxa on which they are based. New terms of this sort can be formed by adding to an appropriate generic root either the suffix -lith (e.g. sphenolith) or the suffix -id plus coccolith, murolith, planolith, or placolith (e.g. reticulofenestrid coccoliths).

Only modern usage is given here and many terms have undergone a complex evolution of meaning so that literature usage needs to be interpreted with caution; this applies particularly to the terms cricolith, cyrtolith, discolith, rhabdolith, and tremalith.

Caneolith {Braarud *et al.* 1955*a*, 1955*b*} – Syracosphaeraceae, endothecal coccolith. (N.B. The terms complete/incomplete caneoliths have been used; see Appendix 1).

Cricolith {Braarud *et al.* 1955*a*, 1955*b*} – Pleurochrysidaceae, ring-shaped placolith.

Cyrtolith {Braarud *et al.* 1955*a*, 1955*b*} – Syracosphaeraceae, exothecal coccolith.

Discolith {Huxley 1868} – Pontosphaeraceae, murolith without flanges.

Helicolith – Helicosphaeraceae, coccoliths with helical flange.

Lopadolith {Lohmann 1902} – high rimmed equatorial murolith of *Scyphosphaera*.

Osteolith {Halldal and Markali 1955} – whorl coccoliths of *Ophiaster*.

Pappolith – Papposphaeraceae.

Podorhabdid coccolith – Podorhabdaceae.

Protolith – Stephanolithaceae, Parhabdolithaceae (cf. Bown 1987).

Rhabdolith {Schmidt 1870} – Rhabdosphaeraceae, planoliths with or without spines.

Scapholith {Deflandre and Fert 1954} – *Calciosolenia*, *Anoplosolenia* (alternative term rhombolith).

Tremalith {Lohmann 1913} – Hymenomonadaceae, vase-shaped murolith.

Reticulofenestrid coccolith {Young 1989} – *Reticulofenestra* and descendants.

Coccolithid placolith {Jordan *et al.* 1995} – Coccolithaceae.

(N.B. See also the sections on nannoliths and holococcoliths, and Appendix 2, for related terms).

ULTRASTRUCTURE RELATED TERMS

1. Types of ultrastructural component

These are based largely on Young and Bown (1991).

Element – apparently discrete component of a coccolith. This is an observational term; several elements may unite to form a crystal-unit.

Crystal-unit – a group of elements from different cycles in crystallographic continuity. These are the fundamental components of coccoliths and their identification is a key objective of ultrastructural reaserch.

Segment – one symmetrically repeated part of the coccolith, including elements from each cycle, consisting of one or more crystal-units.

Lamina – platy sub-structure within a crystal-unit (e.g. *Braarudosphaera*).

Contact-surface – plane of contact between two elements (alternative term attachment surface; see Appendix 1).

Suture – trace of contact-surface on surface of coccolith.

Cycle – ring of elements or crystal-units.

Tier – one of a set of vertically superposed cycles (e.g. *Arkhangelskiella*, *Lapideacassis*).

2. Element shapes

N.B. a,b,c are three orthogonal axes, with any orientation.

Block – nearly equidimensional element (abc).

Tile – broad and thin element (ab > c. N.B. *Plate* has been used in this sense but we prefer to use it for larger structures, not for single elements).

Lath – elongate and wide element (a > b > c).

Rod – elongate and narrow element (a > bc)

Wedge – tapering nearly equidimensional element.

Petal/petaloid element – tapering broad and thin element.

Ray – tapering elongate and wide element.

Spine – tapering elongate and narrow element.

Granule – small and irregular or variably shaped element (e.g. blanket elements of *Helicosphaera*, spine-forming elements of *Cretarhabdus*). N.B. *Crystallite* has been used in this sense but we prefer to use it only for holococcolith elements.

3. Element modifications

Curvature – curving of elements. *Laevogyre* – elements curve to the left when traced radially outward. *Dextrogyre* – elements curve to the right when traced radially outward. *Straight* – elements not curved.

Node – block-shaped projection from element.

Keel – lath-shaped projection from element.

Ridge – rod-shaped projection running along element.

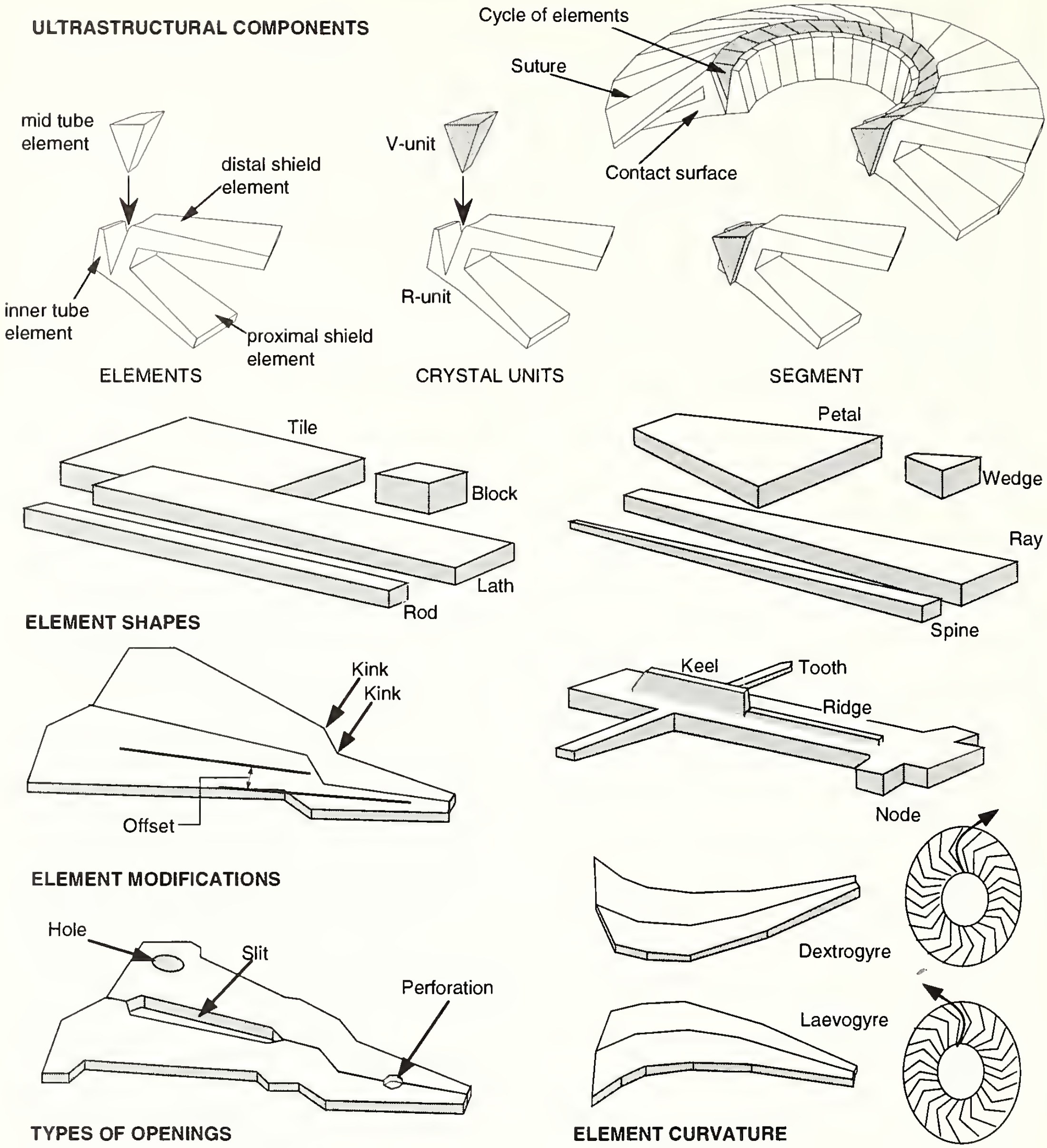
Tooth – rod or wedge-shaped projection from element.

Kink – angular bend in element.

Offset – displacement of an element from radial growth due to a double kink.

4. Special structures

Scissor-structure {Young 1992*b*} – crystal-unit structure formed of two elements growing at only slightly different angles, and forming a two-layered shield (e.g. *Coccolithus* upper and lower proximal shield elements; Text-fig. 6) or tube (e.g. *Toweius* inner and outer tube elements; Text-fig. 6).



TEXT-FIG. 4. Ultrastructural components, elements shapes, element modifications, openings and curvature.

Cross-over zone {Young 1992*b*} – belt around which two cycles of crystal-units cross (this usually corresponds to the proto-coccolith ring, e.g. *Coccolithus*; Text-fig. 6).

5. Openings

Canal – narrow elongate opening within a coccolith or nannolith (Text-figs 10, 14).

Cavity – broad opening within a coccolith or nannolith (Text-figs 10, 14).

Common opening – opening formed by several individuals, i.e. the space within a coccosphere or group of associated nannoliths.

Depression – pit on the surface of a coccolith or nannolith.

Hole {Farinacci 1971} – opening running through one element (e.g. *Pemma basquensis*).

Opening – general term for any space not filled by elements.

Perforation {Farinacci 1971} – small opening between two or more elements.

Slit – elongate perforation (e.g. *Emiliania*).

TERMS FOR DESCRIBING COCCOLITH RIMS

1. *Parts of rims*

Each of these parts may be formed of a single cycle of elements, part of a cycle or several cycles.

Shield – broad (sub-)horizontal structure (placoliths).

Tube – (sub-)vertical structure between two shields (placoliths).

Wall – (sub-)vertical structure not associated with shields (muroliths).

Flange – (sub-)horizontal protrusion from rim.

Collar – (sub-)vertical protrusion from rim (may occur on proimal or distal surface).

Crown – discontinuous/beaded collar.

2. *Directions on the rim*

These are based largely on Black (1972).

Radial – direction in the surface of the baseplate perpendicular to its margin: *inward-outward* – toward-away from centre.

Tangential – direction in the surface of the baseplate parallel to its margin.

Clockwise/dextral/right – anticlockwise/sinistral/left – senses of direction as seen in distal view. We recommend: use of *clockwise/anticlockwise* as the clearest of these terms for general purposes; use of *dextral/sinistral* when it is wished to emphasize particularly that this is the orientation as seen in distal view.

Vertical – direction perpendicular to the baseplate: *up/down* distal-proximal directions.

Flare and *taper* – divergence of orientation from horizontal/vertical in the radial direction. *Flare* surfaces diverge upward, producing *obconical/funnel-shaped* bodies. *Taper* surfaces converge upward, producing *conical bodies.*

3. *Element arrangement as seen in side view*

Imbrication/inclination – divergence from horizontal in the tangential direction. Imbrication is applicable to a cycle of elements, inclination to individual elements.

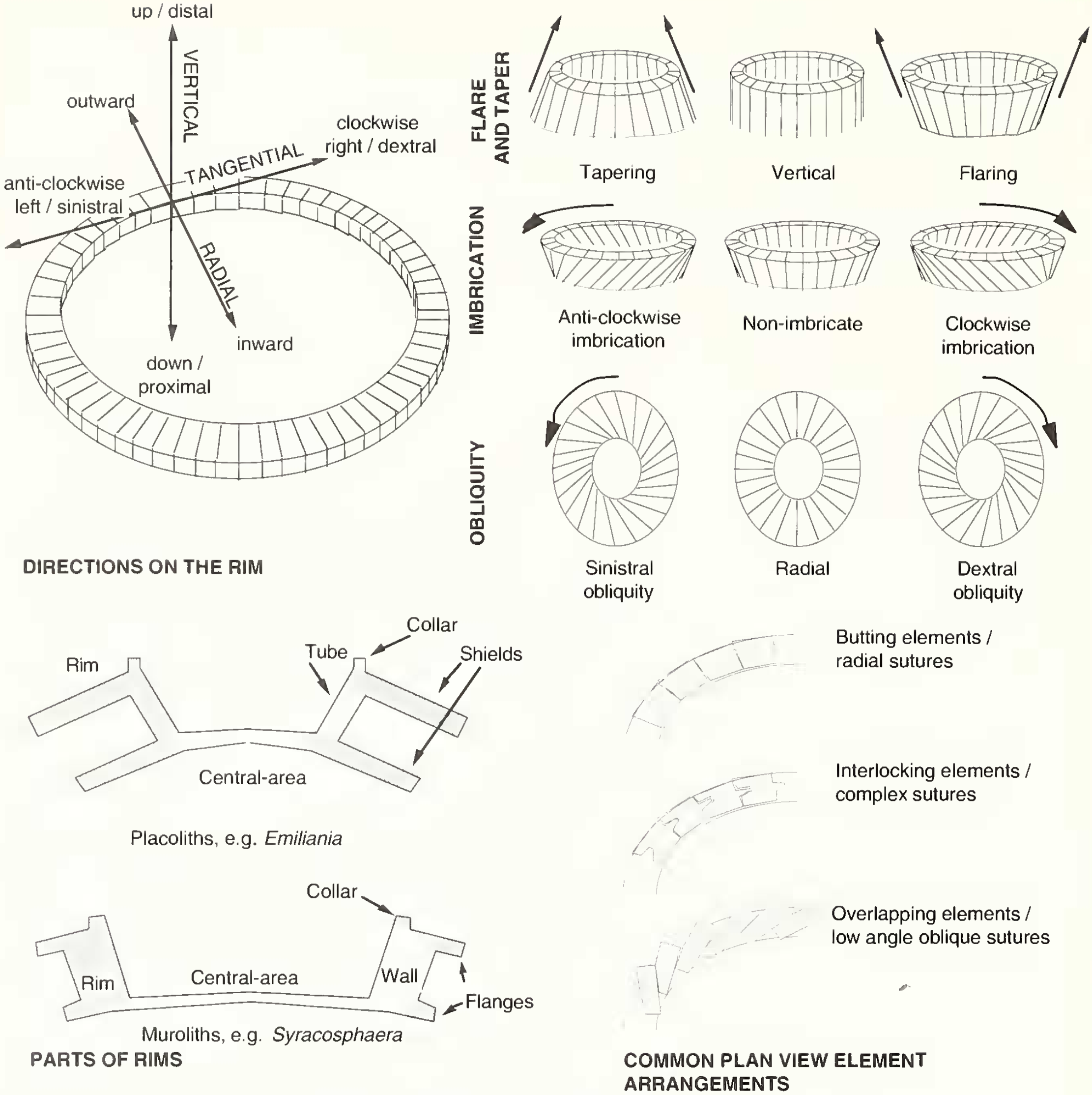
Clockwise/anticlockwise imbrication – offset of upper part of element from lower.

Imbrication angle – angle of contact-surface from the *horizontal*. *High-angle* – sub-vertical contact-surfaces. *Low-angle* – sub-horizontal contact-surfaces.

Zeugoid rim – rim with high-angle imbrication, and without distinct shields (alternative terms loxolith rim, zygodiscid rim; see Appendix 1).

4. *Element arrangement as seen in plan view*

Obliquity – horizontal divergence from radial direction (alternative term precession; see Appendix 1).



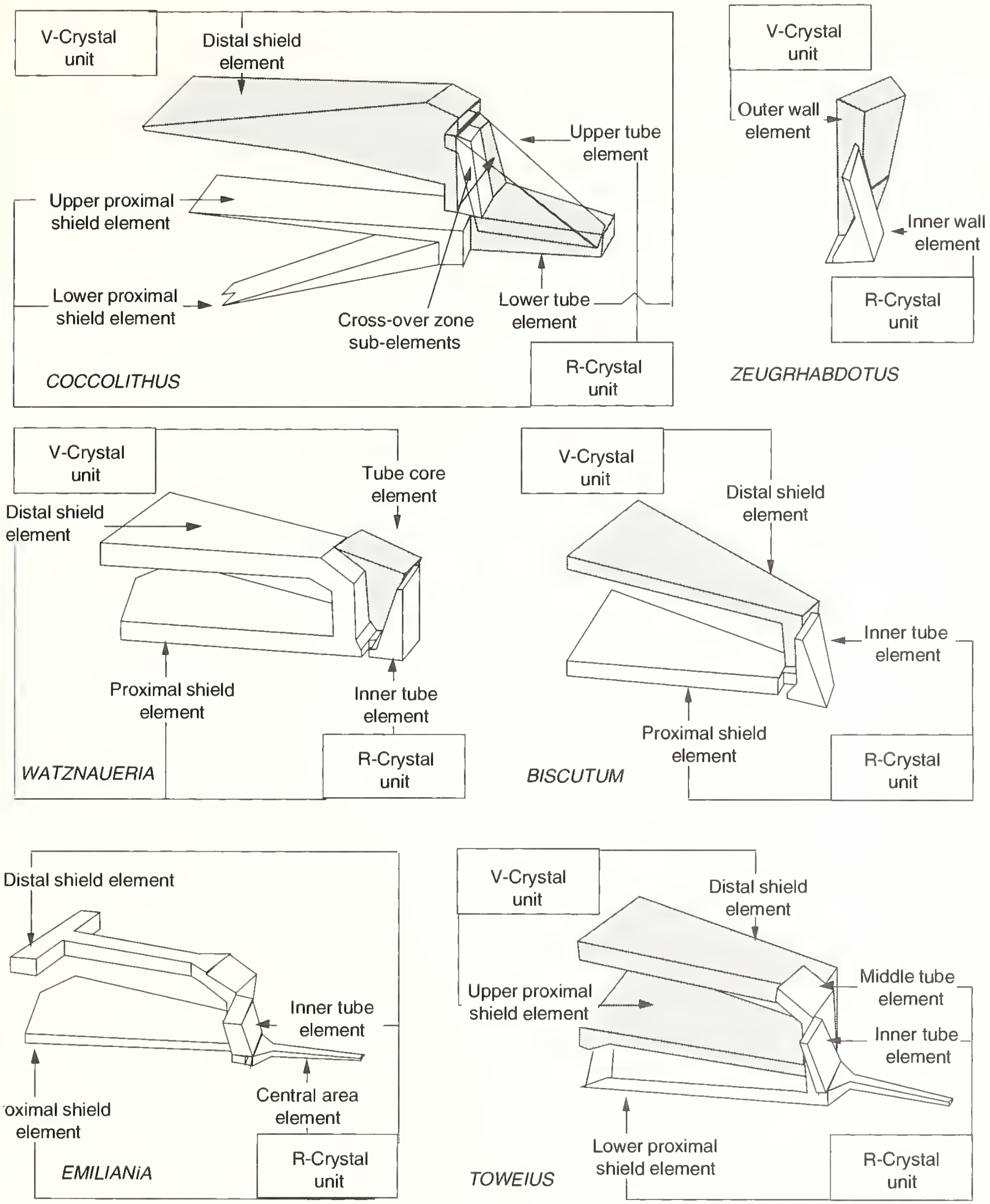
TEXT-FIG. 5. Terms for describing rim structures.

Dexral/sinistral obliquity – deflection from radial of outer part of element relative to inner part, as seen in distal view. Note that elements will show opposite apparent senses of obliquity in distal and proximal view. This can be described as follows: a dextrally oblique cycle displays clockwise obliquity in distal view but anti-clockwise obliquity in proximal view.

Butting – elements with simple (sub-)radial sutures.

Interlocking – elements with complex sutures.

Overlapping – elements with low angle oblique sutures (N.B. This pattern has been described occasionally as imbrication, but we prefer to use imbrication for description of vertical structures).



TEXT-FIG. 6. Terms for identification of elements – with interpreted homologies. Each figure represents one segment of a coccolith. The six examples are representative of major heterococcolith groups. Since the structure of many other coccoliths has not been worked out in detail yet, comparable terminology cannot yet be given for them.

5. Identification of elements

For description and discussion, the various elements/cycles of elements need to be identified. This is best done by reference to the location of the elements using the set of orientation and structure terms given above. Examples are given in Text-figure 8. Element shape is not recommended as an alternative since it is easily altered by diagenesis, intra-specific variation and evolution.

CENTRAL-AREA STRUCTURES

1. Structural types

Conjunct {Young 1992*a*} – formed from crystal-units of the rim structure, such as *Gephyrocapsa* (bridge and grill), *Helicosphaera sellii* (bar), *Kamptnerius* (plate), *Watznaueria biporta* (bar) (alternative term optically continuous structure; see Appendix 1).

Disjunct {Young 1992*a*} – formed from crystal-units discrete from the rim structure. such as *Arkhangelskiella* (plate), *Coccolithus pelagicus* (bar), *Helicosphaera seminulum* (bar), *Watznaueria britannica* (bar) (alternative term optically discontinuous structure; see Appendix 1).

2. Orientation in profile

Basal – occurring on the proximal surface.

Elevated – occurring above the proximal surface.

Vaulted – cone-shaped, rising from the rim toward the centre.

Longitudinal – parallel with long axis of (elliptical) coccolith.

Planar – flat, not vaulted.

3. Orientation in plan view

Transverse – parallel with short axis of (elliptical) coccolith.

Diagonal – inclined relative to axes. Angle should be measured from transverse direction: *low angle* – near to transverse direction; *high angle* – near to longitudinal direction.

Dextral/sinistral – inclined to the right/left of the long-axis as seen in distal view. N.B. As with element obliquity the terms dextral/sinistral are preferred for decribng orientations which appear different in proxmal and distal view.

Relative width – width of central-area relative to rim width: *wide* – central-area width more than twice rim width; *normal* – central-area width one to two times rim width; *narrow* – central-area width less than rim width.

4. Structures spanning central-area

Arm – part of crossbar, bridge or cross running from centre of coccolith to edge of central-area (alternative terms limb, spoke; see Appendix 1).

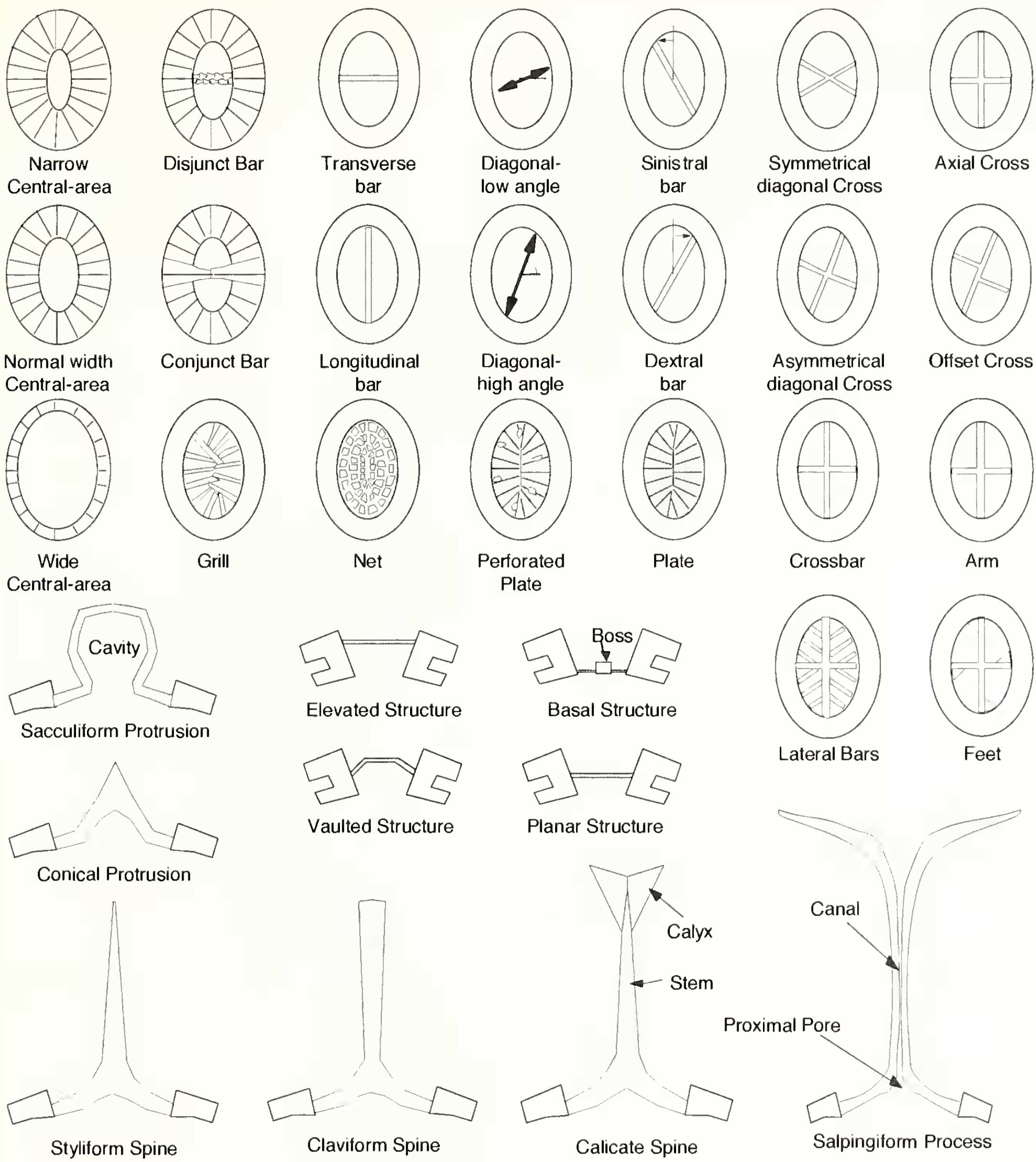
Bar – any elongate central-area structure. N.B. This is a general term. When it is useful to be more specific, terms such as longitudinal bar, cross-bar, and arm can be used (alternative term jugum; see Appendix 1).

Blanket – covering of small elements on distal side of central-area (e.g. *Helicosphaera*, *Coccolithus*).

Bridge – elevated bar spanning the central-area (e.g. *Gephyrocapsa*).

Cross-bar – bar spanning the central-area.

Cross – pair of cross-bars meeting in centre. *Axial cross* (abbreviation +), cross-bars longitudinal and transverse. *Diagonal cross* (abbreviation X) cross-bars diagonal; may be *symmetrical* or *asymmetrical* relative to the axes. *Offset cross* – cross with an offset between the arms of one, or both, of the crossbars (e.g. *Chiasmolithus*).



TEXT-FIG. 7. Central area structures.

Foot – broadening of bar as it meets the rim (e.g. *Cruciplacolithus tenuis*).
Lateral bar – bar running from rim to a cross bar (e.g. *Retecapsa*).

5. *Structures closing central-area*

Central opening – opening at centre of coccolith, may be spanned by bars or other central-area structures, but not by a continuous structure such as a grill or plate.

Closed central-area – central-area without a central opening.

Grill – system of bars closing central-area (e.g. *Emiliania*).

Net – mesh-like structure closing central-area (e.g. *Reticulofenestra*, *Cribrosphaerella*) (alternative term cribrate central-area; see Appendix 1).

Open central-area – central-area without any structures.

Plate – continuous or nearly continuous structure closing central-area.

Perforated plate – plate with perforations (e.g. *Arkhangelskiella*).

6. *Processes*

Calyx – flaring structure at tip of process (e.g. *Podorhabdus*, *Papposphaera*).

Boss – low process, height similar to or less than width (alternative term knob; see Appendix 1).

Process – general term for any structure rising from the central-area.

Protrusion – broad low process, with height similar to width, and width near that of entire central-area. Types: *conical* – cone-shaped protrusion (e.g. *Acanthoica*); *sacculiform* – sac-like protrusion with more-or-less rounded upper part (e.g. *Algirosphaera*). (N.B. *labiatiform* has been used for the elongate double-lipped sacculiform protrusions; see Appendix 1).

Spine – elongated process, height greater than width (alternative term column; see Appendix 1). Types: *styliform* {Halldal and Markali 1955} – spine tapers toward the distal end; *claviform* {Halldal and Markali 1955} – spine has blunt end, without calyx. (N.B. helatoform has been used for nail-shaped processes; see Appendix 1); *calicate* – spine is surmountd by a calyx; *salpingiform* {Braarud *et al.* 1955*a*, 1955*b*} – spine (or protrusion) trumpet-shaped (e.g. *Discosphaera*).

Stem – part of process below calyx.

Cavity – wide opening within process (e.g. *Podorhabdus grassei*, *Algirosphaera robusta*).

Canal – narrow opening running along length of process.

Proximal pore – opening of canal, on proximal side of central-area.

CRYSTALLOGRAPHY

1. *Crystallographic orientation*

Calcite c-axis orientation can be summarized using the following terms, based on Young and Bown (1991), and Young *et al.* (1992). N.B. Actual orientations depart significantly (up to 30°) from true vertical and radial.

V-unit {Young and Bown 1991} – crystal-unit with sub-vertical orientation of c-axis.

R-unit {Young and Bown 1991} – crystal-unit with sub-radial orientation of c-axis, relative to its point of origin (nucleation) on the proto-coccolith ring.

T-unit {new} – crystal-unit with sub-tangential orientation of c-axis (e.g. Braarudosphaeraceae, Polycyclolithaceae).

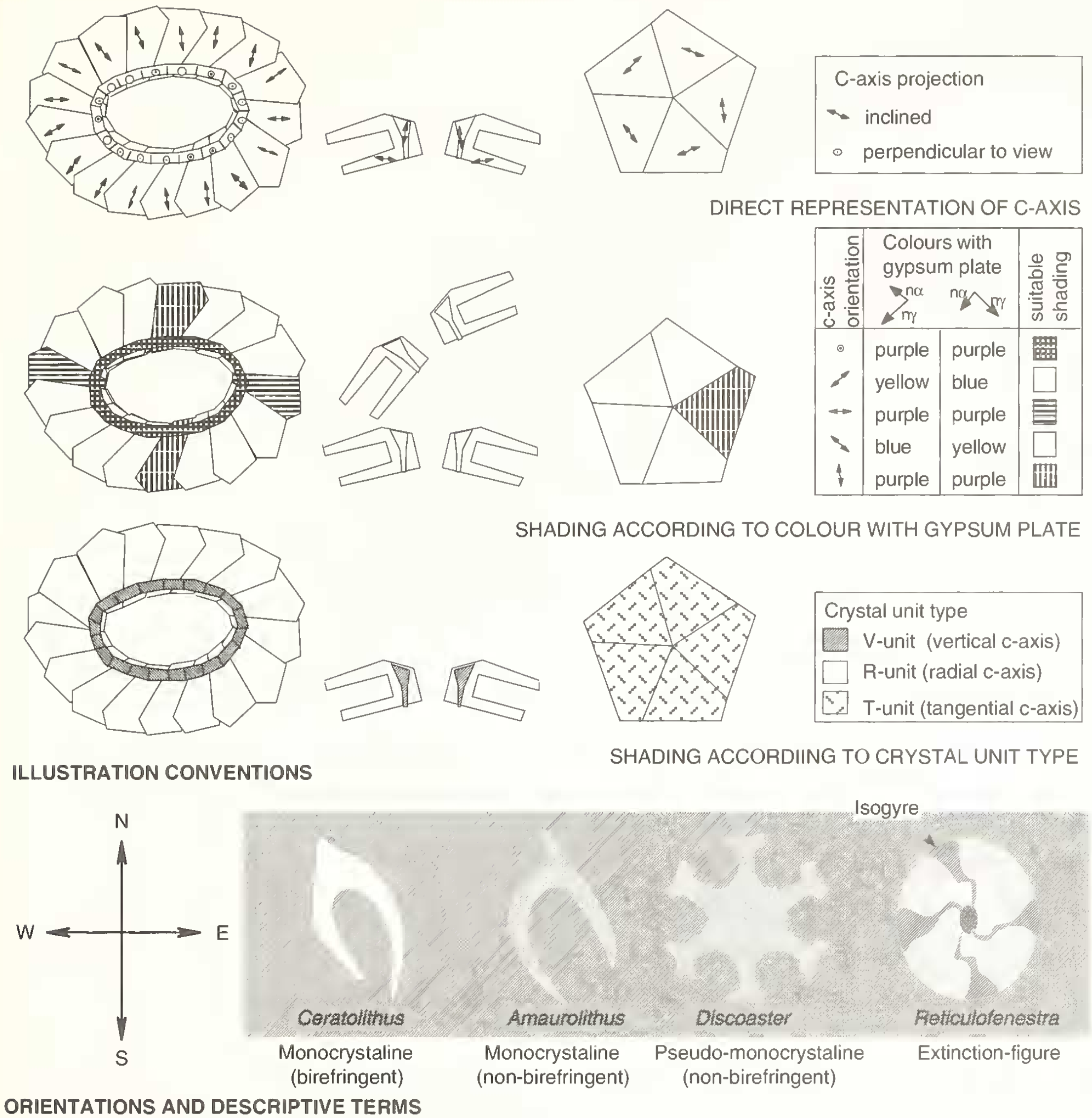
Compound – formed of several crystal-units. such as in *Micula*, *Discoaster*.

Pseudo-monocrystalline – formed of several crystal-units with parallel c-axes, but non-parallel a-axes, such as in *Discoaster*. These behave optically as single crystals, but will not fuse into a single crystal during overgrowth.

Monocrystalline – formed of a single crystal-unit, and so all elements have identical crystallographic orientation of c- and a-axes and overgrow as one unit, e.g. apical spine of *Sphenolithus heteromorphosus*, entire nannoliths of *Florisphaera*, *Marthasterites*, *Minylitha*, *Ceratolithus*.

2. *Graphical conventions for indicating crystallographic orientation*

Symbols – a single symbol per element can indicate c-axis direction (Text-fig. 8).



TEXT-FIG. 8. Crystallography: the diagrams showing illustration conventions are based on *Watznaueria* (plan and side views) and *Braarudosphaera*; the figures in the dark box represent the appearance of nannofossils in the light microscope, with cross-polarized light.

Shading – to illustrate directly observations made with a gypsum plate, hatching can be used – vertical and horizontal for parts in extinction (purple). Diagonal for birefringent parts (blue and yellow). The direction of diagonal hatching should of course be based on the c-axis orientation and since the gypsum plate orientation varies between microscopes the relationship between observed colour (blue, yellow) and c-axis direction has to be determined for each microscope.

Unit type shading – for illustrating structure it is convenient to apply the same shading to all the elements of one crystal-unit cycle in all views of the nannolith. For this the following scheme is recommended: V-units stipples; R-units blank; T-units dashes.

3. *Light microscopy based terms*

Birefringent/non-birefringent – appearing bright/dark between cross-polars. N.B. A coccolith or part of a coccolith can only appear non-birefringent in one orientation (when the c-axis is vertical), so these terms should not be used without explicit description of specimen orientation; e.g. 'discoasters are non-birefringent in plan view'.

Extinction-figure – appearance of a specimen in cross-polarized light, particularly pattern of isogyres.

Isogyre – dark line in cross-polarized light caused by elements in extinction.

North/South, East/West – orientations relative to the microscope body.

INTRASPECIFIC VARIATION

1. *Primary coccolith variation*

As a general principle, styles of variation should be described without reference to inferred causal factors; e.g. 'heavily calcified *E. huxleyi*' is preferable to 'cold-water morphotype'. Terms used here are largely based on Young and Westbroek (1991), Young (1994).

Normally formed – with typical form.

Abnormally formed – departing from normal form in some way, includes all the categories below.

Degree of completion/ontogenetic variation – variation in degree to which the coccolith has grown. (N.B. terms such as juvenile and mature are not recommended for use in this context). *Coccolithogenesis* {Outka and Williams 1971} – process of coccolith development and growth. *Proto-coccolith ring* {Young 1989} – earliest stage of coccolith growth, crystal-units simple without differentiation of elements. *Incomplete coccolith* – elements differentiated but incompletely grown. *Complete coccolith* – all elements fully grown.

Teratological malformation – abnormal form developed as result of irregular growth. N.B. The use of the term malformation to describe other types of variation (e.g. degree of calcification, or growth) is not recommended.

Degree of calcification – primary variation in amount of biogenic calcite incorporated in a coccolith. *Under-calcified* – coccolith with elements markedly thinner than normal for the species. *Normally calcified* – coccolith with elements of normal thickness for the species. *Over-calcified* – coccolith with elements markedly thicker than normal for the species.

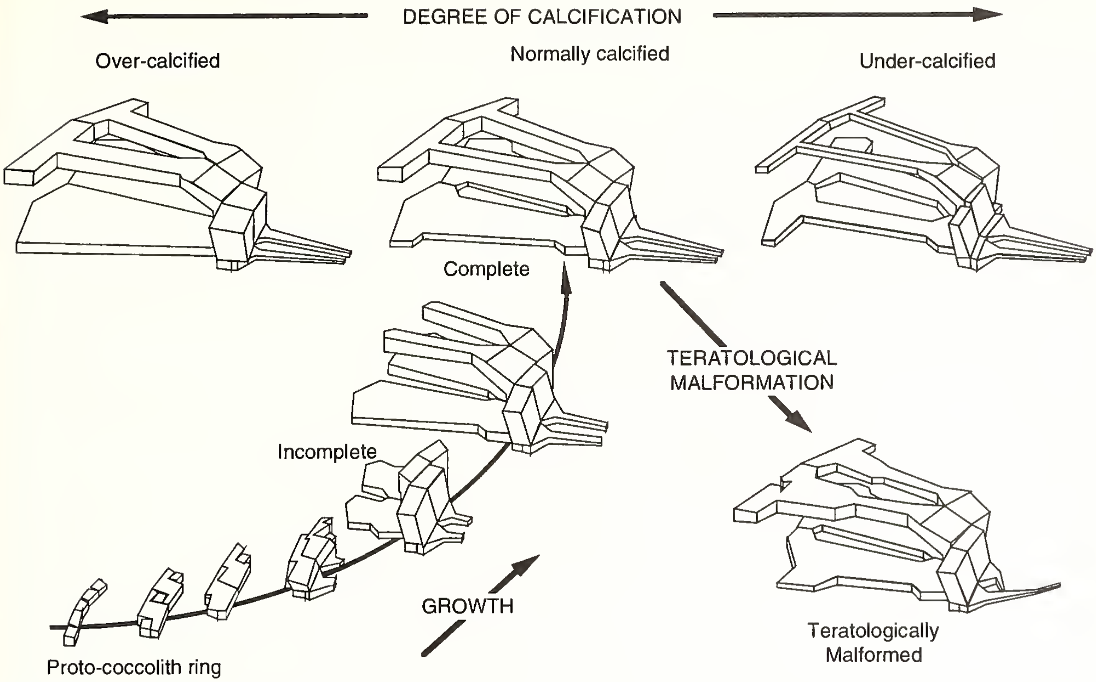
2. *Secondary alteration of coccoliths – diagenetic and water-column effects*

Overgrowth – secondary inorganic growth of calcite on elements.

Etching – secondary inorganic dissolution of calcite from elements. Descriptive scheme, {from Roth and Thierstein 1972; Roth 1983}.

- *X*, *Excellent preservation* – coccoliths appear pristine.
- *E1*, *Slight etching* – serrate outlines, partial dissolution of delicate structures.
- *E2*, *Moderate etching* – irregular outlines, dissolution of most delicate structures and species.
- *E3*, *Strong etching* – much material fragmented, only resistant species left.
- *O1*, *Slight overgrowth* – overgrowth of shield and central-area elements noticeable but does not obscure details.
- *O2*, *Moderate overgrowth* – many elements with large overgrowths, many details obscured.
- *O3*, *Strong overgrowth* – only overgrown elements, identifications very limited.

N.B. Overgrowth and etching commonly both occur in the same sample: this can be shown by codes such as E1-O2. This scheme is primarily for light microscopy; successful electron microscopy requires preservation grades E1, X or O1.



TEXT-FIG. 9. Intraspecific variation. The sub-figures each represent two segments of *Emiliania huxleyi*. The figure only represents primary, biologically induced, variation. Secondary etching and overgrowth can be superimposed on this primary variation, particularly in fossil specimens.

NANNOLITH SHAPES

Nannoliths display a wide range of shapes, including the following types which all occur independently in more than one group. These shape terms are independent of structure, e.g. tetraradiate nannoliths may be formed of one, four or many crystal units.

Dibrachiate – consisting of two sub-parallel arms joined at one end. Includes *horseshoe*, *arrowhead*, and *arcuate* shapes (e.g. *Ceratolithus*, *Amaurolithus*, *Ceratolithina*, *Ceratolithoides* – except *C. verbeekii*).

Compact – more-or-less equidimensional nannoliths. Includes *conical* (e.g. *Sphenolithus*), *obconical* (i.e. inverted cone-shaped, e.g. *Conusphaera*), *cylindrical* (e.g. *Fasciculithus*) and *cubic* (e.g. *Micula*) shapes.

Rod-shaped – elongate, and apparently without a basal disc. Includes *bladed* (e.g. *Lithraphidites quadratus*, *Triquetrorhabdulus carinatus*) and (*sub-*)*cylindrical* (e.g. *Microrhabdulus*) shapes.

Radiate – with radial *symmetry*. N.B. the number of crystal-units may be larger or smaller than the number of rays.

Triradiate – three-fold radial symmetry (e.g. *Marthasterites*, *Trochasterites*).

Tetraradiate – four-fold radial symmetry (e.g. *Micula*, *Quadrum*, *Nannotetrina*).

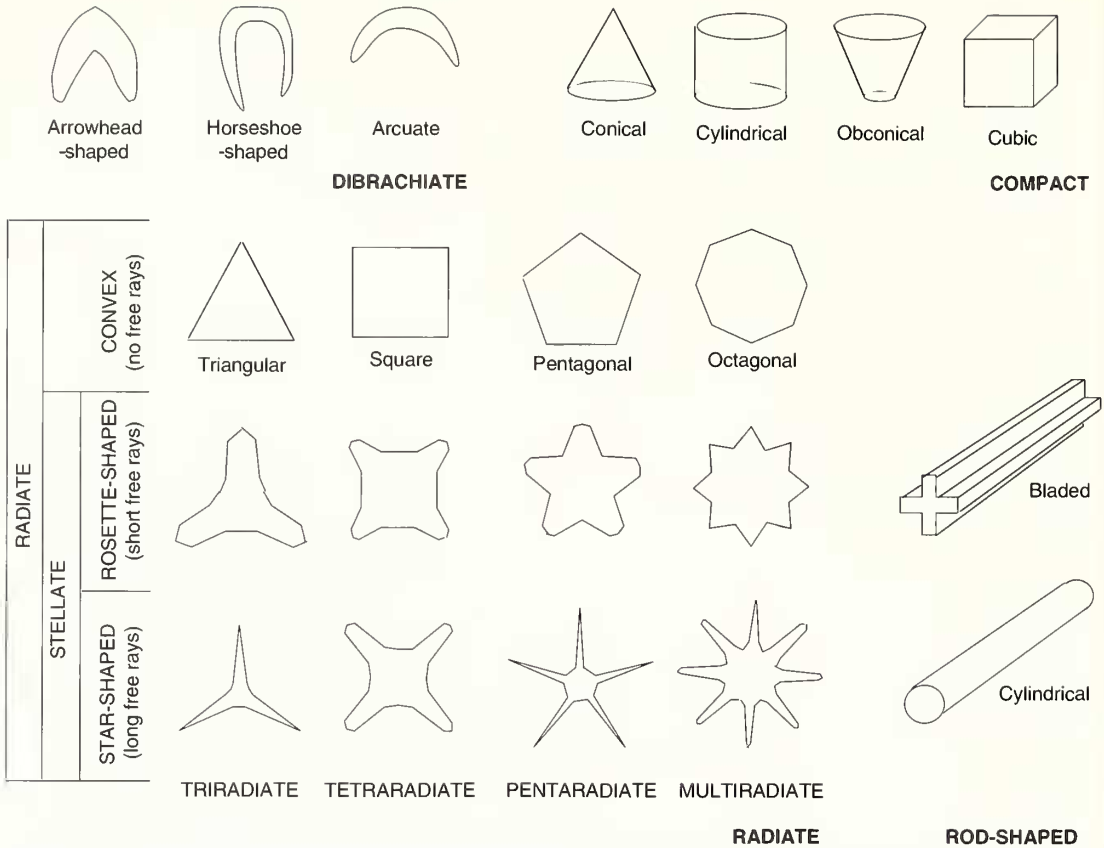
Pentaradiate – five-fold radial symmetry (e.g. *Goniolithus*, *Braarudosphaera*).

Multiradiate – more than five-fold radial symmetry (e.g. many *Discoaster* spp.).

Central body – core part of radiate nannolith where elements are in contact.

Free rays – parts of radiate nannolith extending beyond central body.

Short free rays – length of free rays is less than radius of central body, resulting in a *rosette-shaped* outline.



TEXT-FIG. 10. Nannolith shapes. These terms relate solely to the shape of the nannoliths, not the structure. A cubic nannolith might be formed of one, four, eight or many crystal-units.

Long free rays – length of free rays is greater than radius of central body, resulting in a *star-shaped* outline.

Convex outline – without free rays (e.g. *Braarudosphaera*). Including e.g. *triangular*, *square* and *pentagonal* shapes.

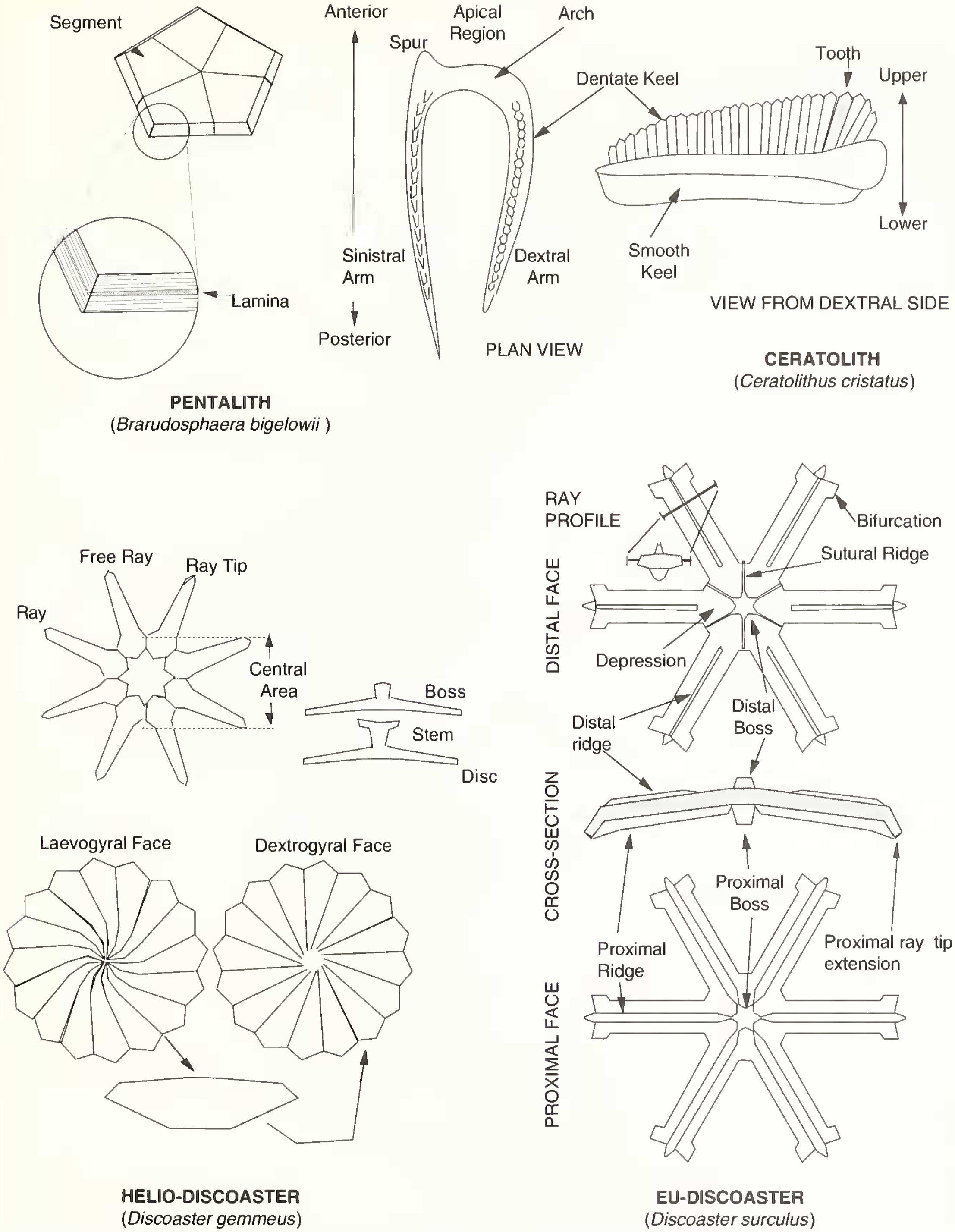
Stellate – with free rays (e.g. *Micrantholithus*, *Discoaster*). Including *rosette* and *star-shaped.*

TERMINOLOGY FOR SPECIFIC HETEROCOCCOLITH AND NANNOLITH GROUPS

For most groups, the general terminology outlined above provides all the terms needed. Some groups, however, have special features which require additional terms, as outlined below. Lapideacassid nannoliths are not covered here: their morphology and sytematics are reviewed by Perch-Nielsen and Franz (1977), and Perch-Nielsen (1985*b*). Terminology for Rhabdolithaceae is mainly covered above, but see also Kleijne (1992). Aubry (1984, 1988*a*, 1988*b*, 1990) reviews terminology for many Cenozoic groups.

Braarudosphaeraceae (*Jurassic–Recent*)

Informal taxon-based name. Pentalith {Gran and Braarud 1935} – nannolith formed by Braarudosphaeraceae (N.B. does not include other nannoliths formed of five elements, e.g. *Discoaster pentaradiatus*).



TEXT-FIG. 11. Special terms applied to Braarudosphaeraceae, Ceratolithaceae and Discoasteraceae. N.B. The terms applied to the description of heterococcoliths may also, where appropriate, be applied to these groups, and *vice versa*.

Lamina – plate-like sub-element of segments.

Segment – one of the five component parts of a pentalith. They appear to be single crystal-units.

Ceratolithaceae (*Late Miocene–Recent*)

Informal taxon-based name. Ceratoliths – dibrachiate nannoliths formed by Ceratolithaceae. Includes *Amaurolithus* nannofossils; does not include the ring-shaped exothecal heterococcoliths.

Orientation. Upper/lower – the more-ornamented surface is designated upper. This division is arbitrary, but it is useful since there is a consistent polarity to structures. With careful through-focussing it is possible to distinguish the two sides by light microsopy. N.B. The terms distal/proximal should not be used since ceratoliths appear to be either intracellular or wrapped around the cell (Norris 1965).

Anterior/posterior – closed end is designated anterior.

Left/right – based on upper view, looking toward anterior end.

Apical region – anterior end of ceratolith; hence terms such as *apical node*.

Arch – part of apical regon connecting the two arms.

Arm – rod-like extension back from apical region.

Rod – rod-shaped structure attached to the nannolith (e.g. *Amaurolithus bizarrus*).

Spur – projection from apical region.

Keel – lath-like structure running along an arm. *Dentate keel* – keel formed of sub-parallel teeth. *Smooth keel* – keel without teeth.

Tooth – rod-like sub-element of a keel.

Wing – plate-like extension from main body of nannolith (e.g. *Amaurolithus ninae*).

Discoasteraceae (*Paleocene–Pliocene*).

Informal taxon-based name. Discoasters – nannolith formed by Discoasteraceae.

Eu-discoaster – typically Neogene and usually star-shaped discoasters, with planar contact surfaces between elements.

Helio-discoaster – typically Paleogene and usually rosette-shaped discoasters, with curved contact surfaces.

N.B. These terms are useful even if formal taxonomic division into the genera *Eu-discoaster* and *Helio-discoaster* is not made. The differences between them are given in Theodoridis (1984) and Aubry (1984).

Orientation. In virtually all discoasters, there are consistent differences between the two faces (Stradner and Papp 1961; Prins 1971; Romein 1979; Aubry 1984; Theodoridis 1984; Self-Trail and Bybell 1995). Many of the Neogene eu-discoasters consistently have one concave and one convex face and, by analogy to coccoliths, these faces have been termed *proximal* and *distal* (e.g. Theodoridis 1984). The two sides are also consistently characterized by various other structures; in particular there are usually sutural ridges on the distal side (Text-fig. 11). These structures can be used to separate the proximal and distal faces of planar eu-discoasters.

In helio-discoasters the rays are usually curved, so *laevogyral* and *dextrogyral* faces can be distinguished. Moreover, the curvature is usually stronger on the laevogyral surface. It is not, however, certain which of these faces corresponds to the proximal face in eu-discoasters, and they have varying relationships to discoaster concavity. Hence, the terms proximal and distal have been applied rather inconsistently in this group (compare Stradner and Papp 1961, Prins 1971 and Romein 1979) and are, perhaps, better avoided.

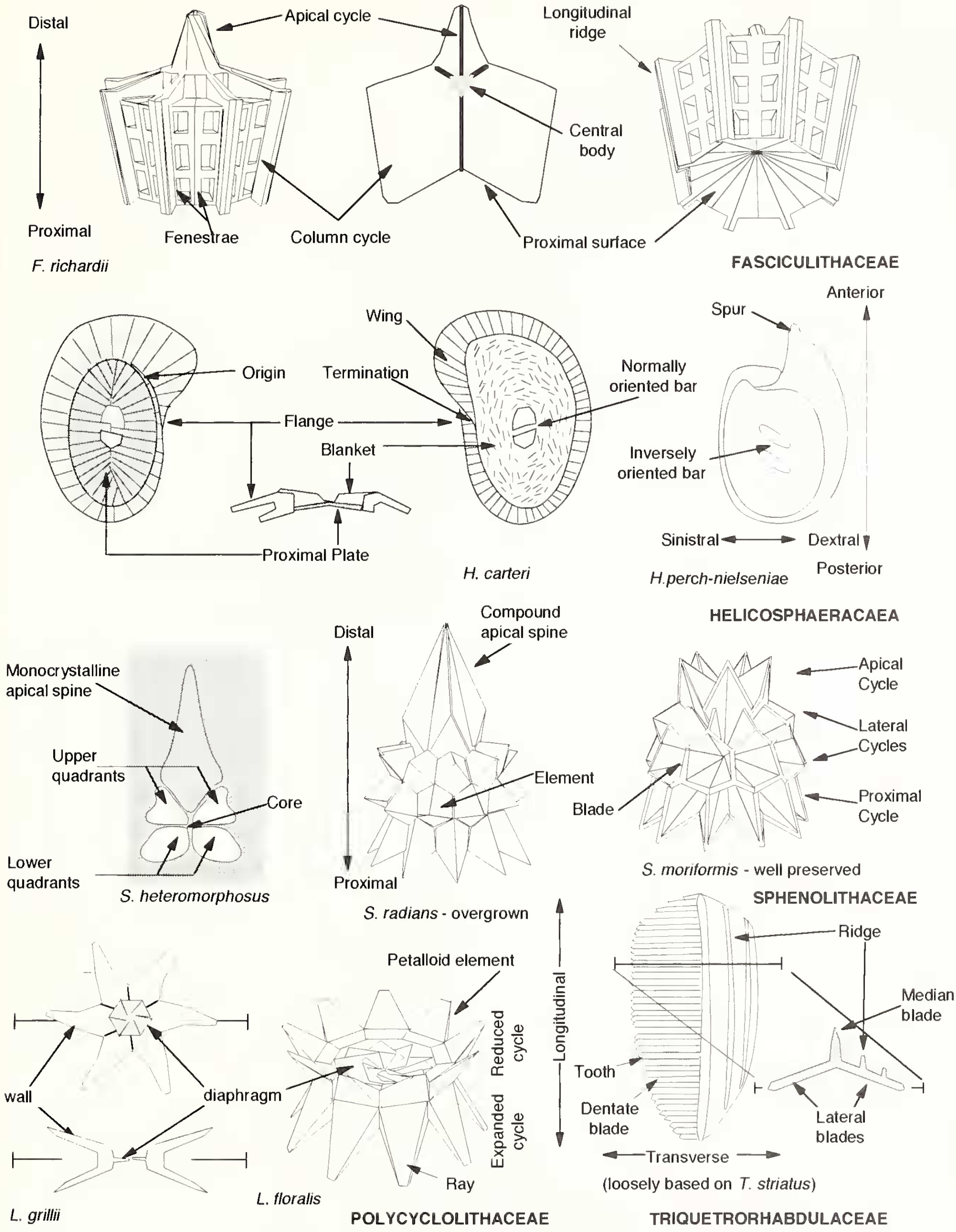
Ray – disc element.

Free ray – part of ray protruding beyond central-area.

Ray tip – outermost part of ray.

Bifurcate tip – ray tip divides into two *bifurcations* (e.g. *D. variabilis*).

Simple tip – ray tip without bifurcation or proximal extension.



TEXT-FIG. 12. Special terms applied to Fasciculithaceae, Helicosphaeraceae, Polycyclolithaceae, Sphenolithaceae and Triquetrorhabdulaceae. N.B. The terms applied to the description of heterococcoliths may also, where appropriate, be applied to these groups, and *vice versa*.

Proximal extension – continuation of the ray downward from the tip (e.g. *D. brouweri*).
Central-area – portion of discoaster with rays in contact.
Contact-surface – surface between adjacent elements (alternative term attachment surface; see Appendix 1).
Disc – main part of discoaster, excluding bosses or stems.
Boss – low distal or proximal protrusion from centre of disc (alternative term knob; see Appendix 1).
Rosette-shaped – discoaster with short free rays (Text-fig. 10).
Segment – ray and associated boss or stem elements.
Stem – high distal or proximal protrusion from centre of disc (e.g. *Discoaster kuepperi*).
Star-shaped – discoaster with long free rays (Text-fig. 10).
Sutural ridge – ridge running along suture.

Fasciculithaceae (*Paleocene–Early Eocene*)

Informal taxon-based term. Fasciculith – nannolith formed by Fasciculithaceae.
Orientation. The concave end of the nannolith is assumed to be proximal.
Apical cycle – distal cycle of fasciculith. (Alternative term cone, see appendix).
Central body {Romein 1979} – optically distinct body occurring in the centre of fasciculith.
Column cycle – proximal cycle of fasciculith, usually forms most of the fasciculith.
Fenestra – regular depression on fasciculith.
Longitudinal ridge – ridge parallel to length of fasciculith.
Proximal surface – lower surface of fasciculith.

Helicosphaeraceae (*Eocene–Recent*)

Informal taxon-based term. Helicolith – nannolith formed by Helicosphaeraceae.
Orientation. The asymmetry of helicoliths allows more precise description of orientation than for most other coccoliths.
Anterior – end with origin of flange and usually with broader flange on distal side often with distinct wing or spur (alternative term pterygal; see Appendix 1).
Posterior – opposite end to anterior (alternative term antipterygal; see Appendix 1).
Detxral/sinistral – right/left sides of helicolith as seen in distal view with anterior end upwards. As with other uses, the terms dextral/sinisral are recommended in place of left/right for terms referring to one particular orientation. The wing, when present, is on the sinistral side.
Bar – structure crossing central opening. Types:
- *Conjunct* – developed from rim elements (e.g. *H. carteri*) (alternative terms optically continuous bar, bar, bridge; see Appendix 1).
- *Disjunct* – formed from elements discrete from the rim (e.g. *H. intermedia*) (alternative terms optically discontinuous bar, bridge, bar; see Appendix 1).
- *Normally oriented* – diagonal bar with dextral orientation; i.e. rotated to the right of the long axis in distal view/anterior end on opposite side to the wing.
- *Inversely oriented* – diagonal bar with sinistral orientation; i.e. rotated to the left of the long axis in distal view/anterior end on same side as wing. N.B. Use of the terms normal/inverse is a ubiquitous convention based on their relative abundances.

Blanket {Theodoridis 1984} – mass of elements forming distal cover.
(*Helicoid*) *flange* – rim structure of helicolith (shield is also used by some workers).
Origin – location of first/shortest elements of flange on the proximal side.
Proximal plate – inward radiate elements on proximal side of central-area.
Spur – spike-like expansion of flange near its termination (e.g. *H. recta*).
Termination – location of last elements of flange on the distal side.
Wing – broad expansion of flange near its termination (e.g. *H. carteri*).

Polycyclolithaceae (*Cretaceous*)

Informal taxon-based term. Polycyclolith – nannolith formed by Polycyclolithaceae. Varol (1992) gives a review of the group.

Orientation. Clear distal/proximal polarity has not been demonstrated, so these terms should be avoided.

Diaphragm – plate-like central cycle of elements

Wall – outer part of nannolith, typically formed of two superposed cycles of elements.

Reduced/expanded cycle – smaller/larger of the two wall cycles.

Ray, *petalloid*, *block* – typical shapes of wall elements.

Sphenolithaceae (*Paleocene–Pliocene*)

Informal taxon-based term. Sphenolith – nannolith formed by Sphenolithaceae.

Orientation. The concave end of the nannolith is assumed to be proximal/basal.

Apical cycle – upper part of sphenolith, formed of most steeply inclined cycle of elements. Types: *Monocrystalline* – formed of one crystal-unit; e.g. *S. heteromorphosus*, *S. belemnos*. *Duocrystalline* – formed of two crystal-units; e.g. *S. distentus*, *S. furcatulithoides*. *Compound* – formed of several crystal-units; e.g. *S. radians*, *S. abies*.

Apical spine – elongate extension of apical cycle.

Base – all of sphenolith except the apical spine.

Blade – one of three sub-parts of an element, seen only in well preserved material.

Core – centre of radiation of elements.

Element – basic component of sphenoliths, each element appears to be a single crystal-unit.

Lateral cycles – cycles between apical and proximal cycles, not always present.

Proximal cycle – lowermost cycle of elements.

Upper/lower part – part above/below the core.

Triquetrorhabdulaceae (*Oligocene–Pliocene*)

Orientation. There is no obvious proximal/distal differentiation.

Longitudinal – parallel to length of nannolith.

Transverse – perpendicular to length of nannolith.

Blade – one of the three main sub-parts of the nannolith.

Dentate blade – blade with transverse sub-structure of rod-shaped teeth.

Lateral blade – one of two broader blades nearly in the same plane (e.g. *T. rugosus*).

Median blade – narrowest of three blades.

Ridge – subsidiary longitudinal structure on a blade (e.g. *T. challengeri*).

Wing – blade greatly extended in transverse direction (e.g. *T. finifer*).

Tooth – rod-like part of a dentate blade.

HOLOCOCCOLITHS

1. Terms for parts of holococcoliths

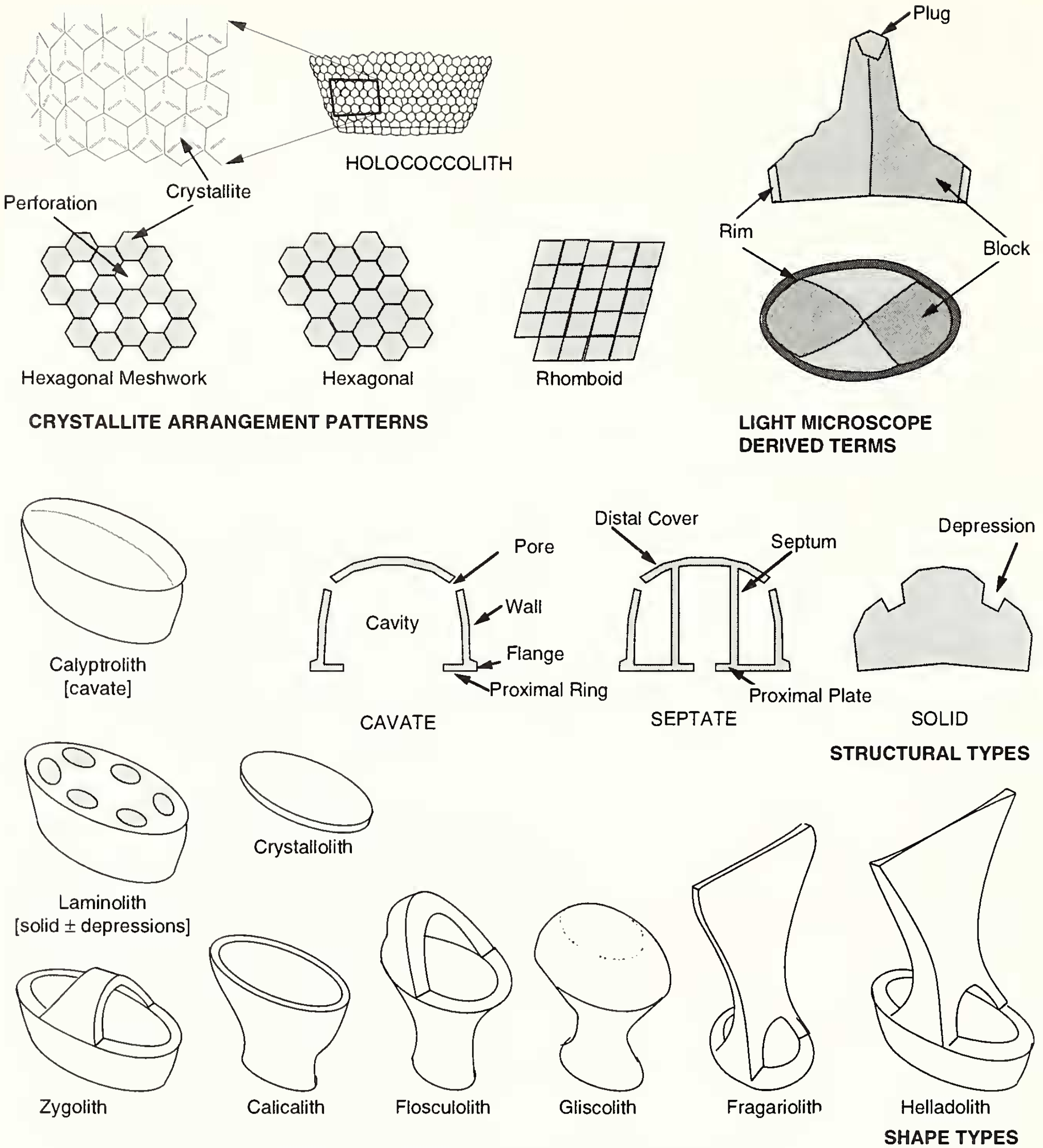
Block – zone of holococcolith that behaves in cross-polarized light as one unit.

Cavity – open central part of holococcolith, not filled by crystallites (e.g. *Calyptrosphaera*, *Zygosphaera*).

Crystallite – individual minute crystal.

Crystallite arrangement – pattern of crystallites visible on a surface. Types: *hexagonal*, *hexagonal meshwork*, *rhomboid*.

Depression – pit on surface, not opening into a cavity.



TEXT-FIG. 13. Special terms applied to holococcoliths.

Distal-cover – distal layer(s) of crystallites, covering cavity (may merge into rim or be discrete from it).

Perforation – opening in wall the size of one crystallite.

Plug – distally positioned block (e.g. *Lucianorhabdus*).

Pore – opening in wall larger than one crystallite (e.g. *Gliscolithus*).

Proximal flange – sub-horizontal protrusion from base of rim.

Proximal-plate – proximal layer(s) of crystallites (nearly) covering base of coccolith.

Proximal-ring – proximal layer(s) of crystallites confined to edge of coccolith.

Rim – peripheral zone discrete in cross-polarized light from the main blocks (typically rim elements have radial c-axes).

Septum – layer(s) of crystallites forming internal wall.

Wall – layer(s) of crystallites forming sub-vertical structure.

2. General terms for description of entire holococcoliths

Cavate – with large cavity inside rim (e.g. *Calyptrosphaera*).

Septate – space inside rim is subdivided by septa (e.g. *Syracolithus quadriperforatus*, *Anfractus harrisonii*).

Solid – coccolith consists essentially of a single mass of crystallites without distinct cavity, or septa, with or without depressions, perforations, or pores (e.g. *Syracolithus catilliferus*) and possibly many fossil holococcoliths.

3. Morphological types

For holococcoliths, unlike heterococcoliths, there are not many useful structural characters, and the special shape terms (e.g. calyptrolith, helladolith) describe morphotypes that almost certainly occur independently in different taxa. So, these terms are purely descriptive terms and independent from taxonomy. They are not much used by palaeontologists and we do not recommend the creation of new terms for fossil holococcolith types. See also Norris (1985), Kleijne (1991) and Jordan *et al.* (1995).

Calicalith {Kleijne 1991} – open cavate, without distal cover (e.g. *Calicasphaera*).

Calyptrolith {Lohmann 1902} – domal cavate, with nearly continuous distal-cover (e.g. *Calyptrosphaera*).

Crystallolith {Braarud *et al.* 1955*a*} – disc-like solid holococcolith formed of one or two layers of crystallites, with low rim (e.g. *Coccolithus pelagicus* phase *hyalinus*).

Flosculolith {Kleijne *et al.* 1991} – cavate with distal opening partially closed by a vaulted distal-cover (e.g. *Flosculosphaera*).

Fragariolith {Kleijne 1991} – proximal plate directly surmounted by blade-like process (e.g. *Anthosphaera fragaria*).

Gliscolith {Norris 1985} – cavate with bulbous distal part (e.g. *Gliscolithus*).

Helladolith {Heimdal and Gaarder 1980} – similar to zygolith but with bridge expanded distally into double-layered leaf-like process (e.g. *Helladosphaera*).

Laminolith {Heimdal and Gaarder 1980} – solid holococcolith formed of several (more than two) horizontal layers of crystallites, with or without perforations/pores (e.g. *Syracolithus catilliferus*).

Zygolith {Kamptner 1937} – with bridge-shaped distal-cover (e.g. *Homozygosphaera*).

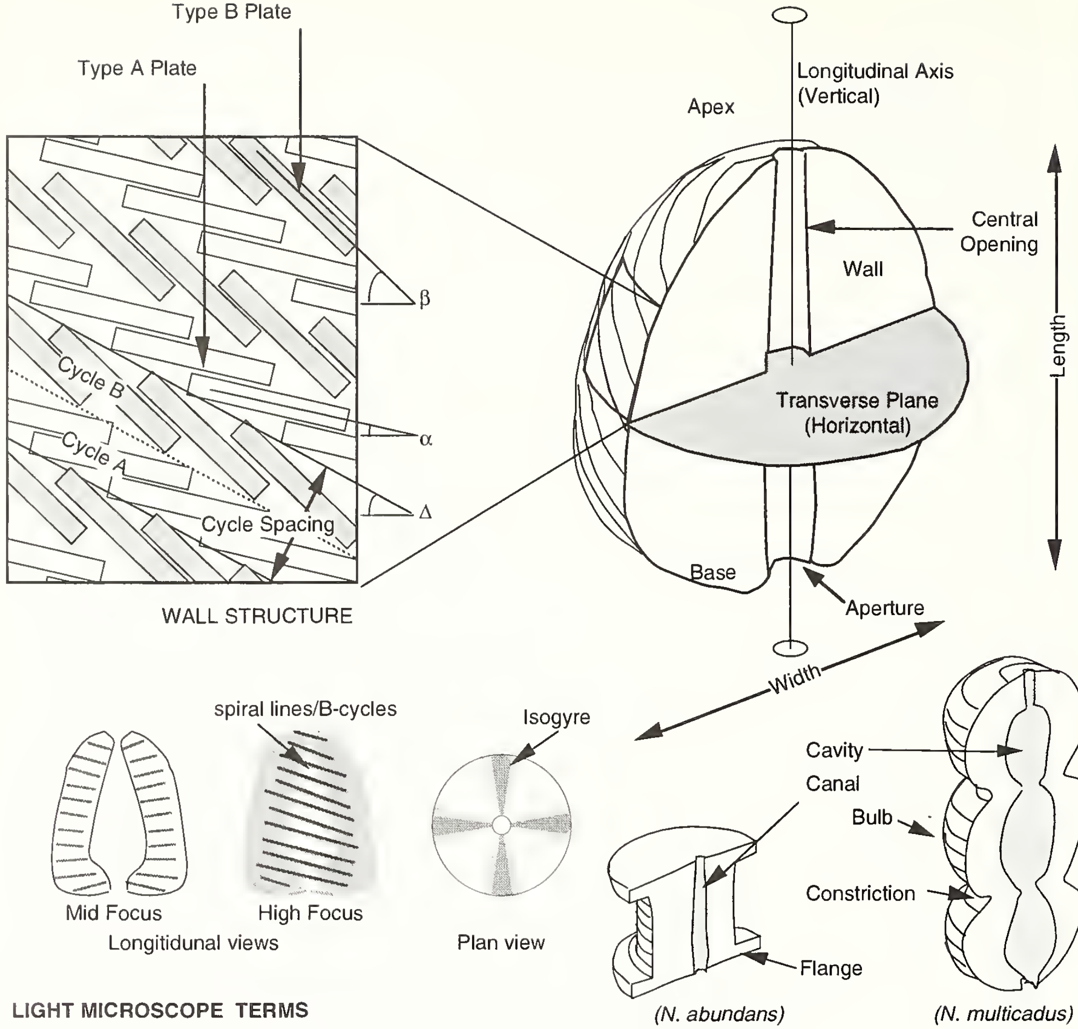
NANNOCONACEAE

Nannoconaceae is a monogeneric group of rock-forming Late Jurassic to Late Cretaceous nannoliths of uncertain affinities. The terminology applicable to *Nannoconus* is reviewed in detail by van Niel (1994), and the following is a list of key terms only.

Informal taxon-based term. Nannoconid.

1. Associations

Groups of associated nannoconid individuals have been found by various workers: Trejo (1960); Colom (1965); Ozkan (pers. comm.). These associations have only a very small common opening and may represent colonial groups of cells (cf. many diatoms) rather than single organisms (cf. typical coccospheres).



TEXT-FIG. 14. Special terms applied to holococcoliths.

Association {van Niel, 1994} – a group of systematically arranged individuals.

Twin {van Niel 1995} – two nannoconid individuals joined at their ends, with ridges and grooves extending across the contact surface.

2. *Orientation*

Rosette {Noël 1958} – association of nannoconids lying side-by-side with their longitudinal-axes radiating from a central point. N.B. It is possible that all rosettes are spherical, but the term sphere is not recommended since this has not been demonstrated, and since nannoconid associations may not be strictly comparable to coccospheres.

Longitudinal axis – axis of rotational symmetry of nannoconid.

Transverse plane – plane perpendicular to the longitudinal axis.

Horizontal – directions within the transverse plane.

Vertical – directions parallel to the longitudinal axis.

Pole – end of nannoconid, point of emergence of symmetry axis: *apex* {Bronnimann 1955} – pole in *N. steinmannii* at narrower end of specimen; *base* {Bronnimann 1955} – pole opposite to apex (broader end in *N. steinmannii*).

Longitudinal view – view of nannoconid parallel to longitudinal axis.

Plan view – view of nannoconid perpendicular to longitudinal axis.

3. General terms

Central opening {Kamptner 1931} – opening running longitudinally through the nannoconid. Types: *canal* – narrow, < 1 μm; *cavity* – wide, > 1 μm; *aperture* {Kamptner 1931} – expression of the central opening at the ends of the specimen.

Bulb {Trejo 1960} – a distinct swelling of the outline (e.g. *N. borealis* – single, *N. paskeutiensis* – double, *N. multicadus* – triple).

Constriction {Deflandre and Deflandre-Rigaud 1962} – external indentation of the wall, between bulbs.

Flange {Stradner and Grün 1973} – horizontal projection around the end of nannoconid. N.B. Flanges may be symmetrical or asymmetrical in end view, and may be present at one or both ends of the specimen.

Wall {Kamptner 1931} – structure enclosing the central opening.

4. Structure

Nannoconids appear to be formed of two types of plates arranged in alternating cycles (van Niel 1992). These cycles appear to spiral around the wall but the precise geometry is not yet clear.

Plate {Stradner and Grun 1973} – basic structural element of nannoconid, single sub-triangular platy crystal (alternative term wedge; see Appendix 1).

Type A-cycle {van Niel 1992} – cycle of plates inclined at a lower angle (*angle α* to the horizontal). These are birefringent in longitudinal view (Perch-Nielsen 1988).

Type B-cycle {van Niel 1992} – cycle of plates inclined at a higher angle (*angle β*) to the horizontal. These cycles are non-birefringent in longitudinal view and form the dark *spiral lines* observed in cross-polars in longitudinal view (Kamptner 1931; Deflandre and Deflandre-Rigaud 1962; Perch-Nielsen 1988).

Angle Δ {van Niel 1992} – angle of the A cycle/B cycle contact to the horizontal. N.B. This is the only angle measurable by light microscopy.

Cycle spacing – repeat distance between cycles perpendicular to angle Δ, i.e. combined thicknesses of A and B cycles.

CALCISPHERES

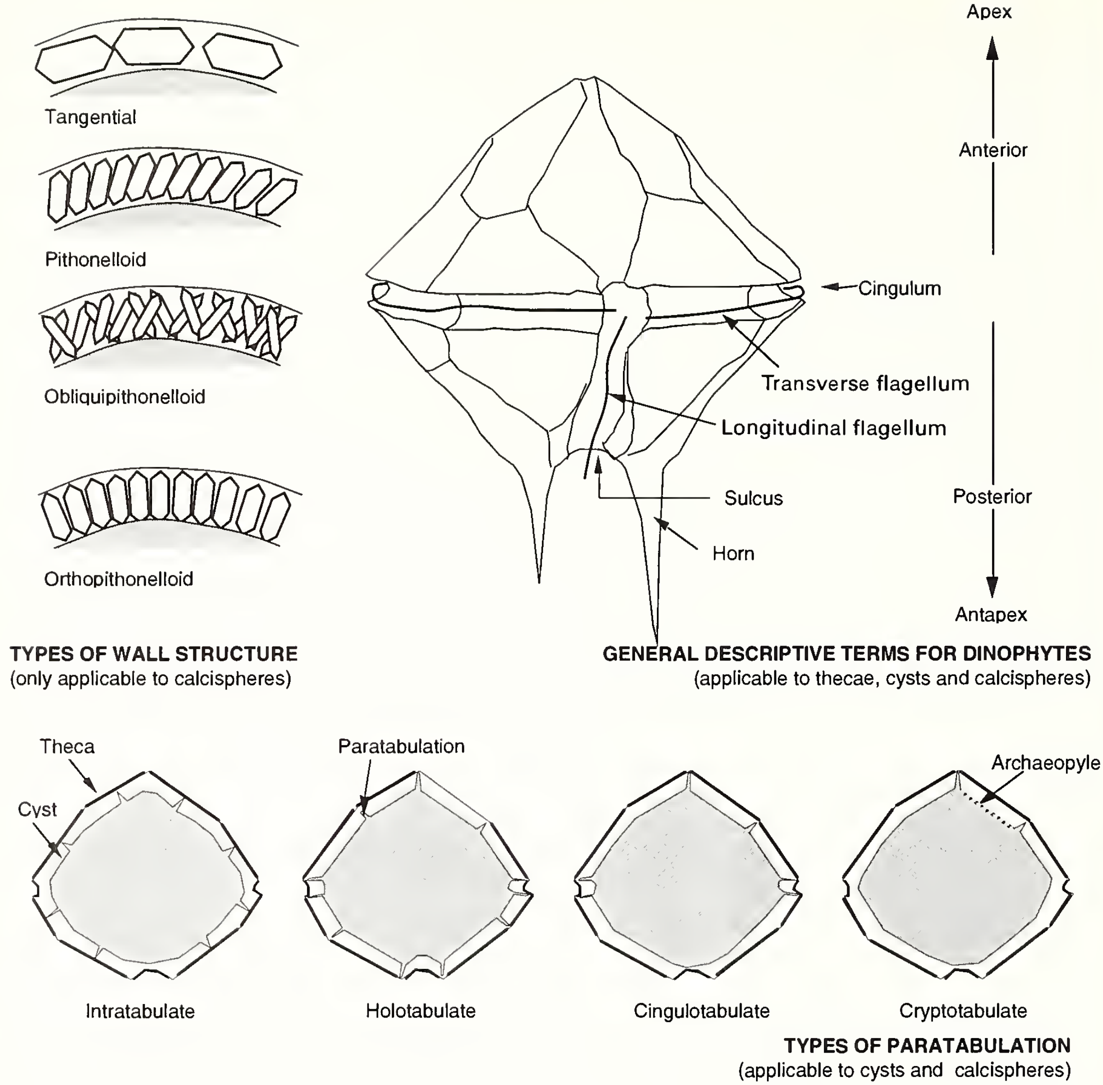
Palaeozoic calcispheres are of uncertain affinity and are not discussed here. Most Mesozoic and Cenozoic calcispheres are now believed to be dinoflagellate cysts. Keupp (1991) gave an English-language synthesis of this group; Janofske and Keupp (1992) gave a brief overview. These workers regard wall structures as the primary basis for classification. Williams *et al.* (1978), Sergeant (1982) and Evitt (1985) summarized the terminology for describing organic-walled cysts, much of which can be directly applied to calcispheres. Only the most important, relevant terms are included here.

1. Orientation

Dinoflagellates have clearly differentiated ends, shown by shape, flagellar disposition, behaviour, etc. Swimming direction is conventionally used to determine front and rear.

Apex/anterior end – front of dinoflagellate when swimming, usually pointed. Almost always contains the archaeopyle.

Antapex/posterior end – rear of dinoflagellate when swimming, usually flaring.



TEXT-FIG. 15. Terms used in the description of calcispheres. N.B. Calcispheres are formed by dinoflagellates and their terminology is independent of that used for other calcareous nannoplankton.

Ventral side – side of dinoflagellate with longitudinal flagellum and sulcus.
Dorsal side – side opposite longitudinal flagellum and sulcus.

2. General terms

Calcisphere – hollow, typically spherical, calcareous nannofossil. Whereas coccospheres are composite structures formed of numerous coccoliths, calcispheres possess a continuous wall.

Cyst – wall formed around dinoflagellate during non-motile, non-vegetative stage. These often show paratabulation but are continuous structures, except for the archaeopyle if present. Most calcispheres are thought to be cysts; however, the thoracosphere of *Thoracosphaera heimii* is formed during the vegetative stage and so is not a cyst.

Dinoflagellate – informal taxon-based term for member of the phylum Dinophyta.

Theca – non-resistant organic wall of motile vegetative stage of dinoflagellates, composite structures formed of plates.

Thoracosphere – informal taxon-based term for calcisphere formed by *Thoracosphaera*. N.B. *T. heimii* has a wall structure of large elements (*c.* 1 μm) with their c-axes tangential to the wall, and randomly aligned.

3. *Wall types*

Oblique/obliquipithonelloid – formed of elements with their c-axes oblique to the wall and variably aligned relative to each other (e.g. *Obliquipithonella multistrata*).

Pithonelloid – formed of elements with their c-axes oblique to the wall and sub-parallel to each other (e.g. *Pithonella sphaerica*, *P.ovalis*).

Radial/orthopithonelloid – formed of elements with their c-axes perpendicular to the wall (e.g. *Calciodinellum*, *Rhabdothorax*).

Tangential – formed of elements with their c-axes tangential to the wall (e.g. *Fuetterella conforma*, *Thoracosphera heimii*).

4. *Paratabulation features*

Archaeopyle – opening for excystment.

Operculum – plate covering the archaeopyle.

Paratabulation – structures on the cyst of a dinoflagellate reflecting the tabulation of the theca. Paratabulation may be developed on the inner or the outer surface of calcispheres.

Cingulum – sub-equatorial channel occupied by the transverse flagellum.

Sulcus – furrow occupied by longitudinal flagellum.

Horn – protrusion from either end of dinoflagellate.

5. *Paratabulation types*

Holotabulate – paratabulation of ridges or edges on the cyst corresponding to plate boundaries on the theca.

Intratabulate – paratabulation of processes on the cyst corresponding to plates on the theca.

Cingulotabulate – paratabulation confined to cingulum and archaeopyle.

Cryptotabulate – paratabulation confined to archaeopyle.

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APPENDIX 1: TERMS THAT WE HAVE NOT USED

The following terms have been used previously in nannoplankton literature but are not used here, for the reasons outlined. In these notes, the term is defined briefly, using our terminology. Then the reason for our not using it is given (see also the introductory section on the choice of terms).

Attachment surface – Contact-surface between two elements. Superfluous synonym; contact-surface seems more objective.

Bar/Bridge (*sensu* Aubry 1988) – as per Theodoridis (1984), but with opposite meanings.

Bar/Bridge (*sensu* Theodoridis 1984) – synonyms of disjunct and conjunct bar, especially for helicoliths. We consider these terms confusing. Also they are of limited application, whereas the terms disjunct and conjunct can be applied to any central-area structure, not just bars.

Coccocylinder {Covington 1985} – cylindrical coccosphere. Superfluous term, numerous coccospheres are aspherical and there is no utility in coining numerous shape related terms.

Coccolithophore – synonym of coccolithophorid, which has priority (see Jordan *et al.* 1995).

Column – often used as a synonym of spine, which we prefer.

Cone – alternative to apical cycle, for fasciculiths. This cycle only forms a conical structure in a few species so we prefer the more neutral term apical cycle.

Complete/incomplete caneoliths {Halldal and Markali 1955} – endothecal coccoliths of *Syracosphaera* with, respectively, three and two flanges. The distinction is useful but there is no real need for these rather obscure special terms. Also, we prefer to use the terms complete and incomplete to describe degree of completion of growth of coccoliths.

Cribrate central area – obscure alternative to net.

Discolith – this term has been used widely for coccoliths with elevated rims but no shields, i.e. muroliths as defined here. We prefer murolith since discolith has also been used with the different sense of 'a coccolith belonging to Pontosphaeraceae'. In addition, the word discolith is potentially misleading.

Geometric – unsuitable alternative of polygonal. Ellipses and circles are just as geometric as are triangles or pentagons.

Heliolith/Ortholith {Deflandre 1950} – these terms for coccolith types were originally defined on the basis of the crystallographic orientation of the main elements. Ortholiths – dominant elements large, with vertical or tangential c-axis orientation (e.g. *Discoaster*, *Braarudosphaera*). Helioliths – dominant elements have approximately radial c-axes giving a 'sphérolithique' appearance (e.g. *Watznaueria*, *Reticulofenestra*). This concept is of limited use since most heterococcoliths are composed of both vertical and radial crystal-units, whilst for many nannoliths the concept of radial and vertical are unclear. As a result, there has been only limited agreement between authors who have used these terms as to which taxa should be included in which group – compare Deflandre (1952), Tappan (1980), Aubry (1984, 1988*a*, 1988*b*, 1990).

Jugum – synonym of bar. Obscure and superfluous.

Knob – synonym of boss, especially for discoasters. We prefer boss, and it has more general application.

Labiatiform {Halldal and Markali 1955} – elongate double-lipped sacculiform protrusion. Unnecessarily specialized term, applying to only one taxon, *Anthosphaera robusta*.

Limb/spoke – synonym of arm. We prefer arm and it has been applied more widely.

Loxolith rim – synonym of zeugoid rim, which we prefer.

Marginal area {many authors} – rim. We prefer rim since it is more suitable for forming complex terms (e.g. proximal rim element), and because marginal area suggests an unimportant feature whereas this is the most important part of many coccoliths.

Nanofossil, *Nanoplankton* – synonyms of nannofossil and nannoplankton. Both nano- and nanno- are etymologically valid prefixes derived from the greek word *nanos* (dwarf). We prefer nanno- on the following grounds: (1) general usage, as noted by the Oxford English Dictionary (2nd edition, 1989), nearly all palaeontologists use nannofossil and many biologists use nannoplankton so this is the *de facto* 'correct' spelling; (2) priority, this was the spelling adopted by Lohmann (1909), when he coined the term nannoplankton; (3) differentiation, the SI use of nano- implies 10^{-9} (e.g. nanometre).

Optically continuous/discontinuous structure – essentially synonyms of conjunct and disjunct. We prefer the latter as they are shorter and less potentially misleading.

Oval, *ovoid* – often used as synonyms of elliptical, but these terms more accurately mean egg-shaped and so are very rarely applicable to coccoliths.

Pterygal, *meta-pterygal*, *pre-pterygal*, *anti-pterygal* {Theodoridis 1984} – orientation terms for helicoliths. Elegant but too obscure for practical use.

Precession {Black 1972} – alternative to obliquity for description of element orientation in plan view. The common scientific use of precession is related to orbital motions which are not analogous to the element orientation. Hence the special use of this term for coccoliths is obscure.

Prymnesiophyte – alternative to haptophyte. Green and Jordan (1994) showed that Haptophyta, rather than Prymnesiophyta is the correct division level name; it follows that haptophyte is preferable to prymnesiophyte as the informal name for members of the division.

Rhombolith {Halldal 1954} – synonym of scapholith. Both are often used; we follow Braarud *et al.* (1955*a*, 1955*b*) in using scapholith.

Stomatal opening and *stomatal coccolith* {Halldal and Markali 1955} – circum-flagellar coccoliths. Stomata implies mouth, and so has unwanted functional implications.

Wedge {Bronnimann 1955} – element of a nannoconid. Bronnimann also used the term plate and this is preferred since it better describes the shape of nannoconid elements as shown by electron microscopy.

Zygodiscid rim – synonym of zeugoid rim, which we prefer.

APPENDIX 2: SUMMARY LISTING OF -LITH WORDS

Numerous special terms have been coined for particular types of coccoliths. These are now used in varying senses, in particular some are used as purely descriptive terms applicable to coccoliths of widely varying structure and taxonomic affinity (e.g. placolith), whilst others are now used only as informal taxon-based terms, i.e. for the characteristic coccoliths from one particular taxon. These terms are, consequently, described in different parts of the main text. For ease of reference, they are all listed here, in alphabetical order. Only the modern/recommended meaning is given here. Readers should be aware that many of these terms have been used in varying ways in the literature. Terms not used in the main text are given in square brackets, [ ].

[*Areolith*] {Norris 1985} – cap-shaped holococcolith with interior ridges and areolae.

[*Asterolith*] {Sujkowski 1931} – obsolete term for stellate nannoliths.

Calicalith {Kleijne 1991} – tube-shaped holococcolith, flaring, open distally.

Calyptrolith {Lohmann 1902} – cap-shaped holococcolith.

Caneolith {Braarud *et al.* 1955*a*, 1955*b*} – endothecal murolith (+/– flanges) of Syracosphaeraceae.

Ceratolith – horseshoe shaped nannolith of Ceratolithaceae.

Coccolith {Huxley 1858} – plate-like calcareous component of haptophyte cell-covering, homologous with organic scale.

[*Cribrilith*] {Halldal and Markali 1955} – perforate murolith of Pontosphaeraceae; in effect a synonym of discolith and so superfluous.

Cricolith {Braarud *et al.* 1955*a*, 1955*b*} – ring-shaped placolith with narrow shields of Pleurochrysidaceae.

Crystallolith {Braarud *et al.* 1955*a*, 1955*b*} – planar holococcolith, rim weak.

[*Cyatholith*] {Kamptner 1948} – obsolete, alternative to placolith.

[*Cyclolith*] {Kamptner 1948} – obsolete, circular placolith.

Cyrtolith {Braarud *et al.* 1955*a*, 1955*b*} – exothecal planolith or inverted murolith of Syracosphaeraceae.

Discoaster – stellate nannolith of Discoasteraceae.

Discolith {Huxley 1868} – murolith of Pontosphaeraceae (has also been used for muroliths in general).

Fasciculith – compact, top-shaped nannolith of Fasciculithaceae.

Flosculolith {Kleijne *et al.* 1991} – flaring, tube-shaped holococcolith, with distal opening partially closed by a vaulted roof.

Fragariolith {Kleijne *et al.* 1991} – holococcolith with simple basal ring and leaf like process

Gliscolith {Norris 1985} – tube-shaped holococcolith with bulbous distal part.

Helicolith – coccolith with helical flange of Helicosphaeraceae.

[*Heliolith*] {Deflandre 1950, Aubry 1984, 1988*a*, 1988*b*, 1990} – heterococcolith with c-axes of main elements radial.

Heliolith – stellate nannolith with birefringent central area, of *Heliolithus* (Paleogene).

Helladolith {Heimdal and Gaarder 1980} – tube-shaped holococcolith with bridge developed into leaf-like process.

Heterococcolith {Braarud *et al.* 1955*a*, 1955*b*} – coccolith formed of crystal-units of complex shape.

Holococcolith {Braarud *et al.* 1955*a*, 1955*b*} – coccolith formed of numerous minute ($< 0{\cdot}1\ \mu m$) crystallites all of similar shape and size.

Laminolith {Heimdal and Gaarder 1980} – laminated disc-shaped holococcolith +/– pores.

Lepidolith {Halldal and Markali 1955} – simple planolith, formed of two elements, of *Gladiolithus*.

Lopadolith {Lohmann 1902} – elevated murolith of *Scyphosphaera*.

Murolith {Young 1992*a*} – any heterococcolith with elevated rim but without well-developed shields

Nannolith {?Perch-Nielsen 1985} – calcareous structure lacking the typical features of hetero- or holococcoliths and so of uncertain affinity.

[*Ortholith*] {Deflandre 1950; Aubry 1984, 1988*a*, 1988*b*, 1990} – nannolith or holococcolith with c-axes of main elements tangential or parallel.

Osteolith {Halldal and Markali 1955} – femur-shaped circum-flagellar coccolith of *Ophiaster*.

Pappolith {Norris 1983} – murolith of Papposphaeraceae.

[*Pentagolith*] {Farinacci *et al*. 1971} – pentagonal coccolith with more than five elements, e.g. *Goniolithus*. These are so rare that the term is redundant.

Pentalith {Gran and Braarud 1935} – stellate nannolith with five segments, of Braarudosphaeraceae.

Placolith {Lohmann 1902} – any heterococcolith with two or more well-developed shields.

Planolith {Young 1992*a*} – any planar heterococcolith, rim not elevated.

[*Porolith*] {Deflandre 1952} – obsolete term for perforate element of *Thoracosphaera*.

[*Prismatolith*] – obsolete term for imperforate element of *Thoracosphaera*.

Protolith {Bown 1987} – murolith with non-imbricate rim of Stephanolithaceae, Parhabdolithaceae.

Rhabdolith {Schmidt 1870} – planolith (+/– spine) of Rhabdosphaeraceae (also has been for spine bearing coccoliths in general).

[*Rhombolith*] {Halldal 1954} – alternative term for scapholith.

Scapholith {Deflandre and Fert 1954} – rhombic murolith of Calciosoleniaceae.

Sphenolith {Deflandre 1952} – nannolith of Sphenolithaceae.

Tremalith {Lohmann 1913} – vase-shaped murolith of Hymenomonadaceae.

Zygolith {Kamptner 1937} – tube-shaped holococcolith with bridge.